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THE VALUE AND PRACTICABILITY OF WILDLIFE CENSUSES ALONG HIGHWAYS

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The dead (and living) animals counted along highways have been summarized in occasional articles and in various progress reports. Whether such counts serve any practical purpose in wildlife research is uncertain. Separate highway censuses of different subjects by the authors from September, 1939, to September, 1941, have provided materials for the present analysis.

DOVE COUNTS ALONG HIGHWAYS

Hilbert R. Siegler

Highway censuses of the mourning dove (*Zenaidura macroura carolinensis*) were made to learn whether such counts would indicate relative abundance by season, and locality, or afford data in a study of the life history. The censuses, averaging 510 miles per month, were made in eastern Texas during 24 months in 1939 to 1941 (except October, 1939). All doves seen within the highway right-of-way were counted (Fig. 1).

The counts for both years agree in that fewer doves were observed in November and February, but disagree in that the fewest (one per 150 miles) were observed in December, 1939, whereas large numbers were observed in December, 1940. In both years doves were most numerous along roadways during May. This does not mean that the population was greatest then, for doves may be more prone to sit along telephone wires and fences, or may be more active in May and thus fly over the highways oftener. The counts are useful if these correlations and exceptions can be interpreted.

The decrease in dove populations along highways during November probably resulted from the hunting season during September and October, but whether this resulted from a decrease in the population or because the doves became wary and were hiding is uncertain.

Other factors also affect the accuracy of highway censuses. Our counts revealed doves as most numerous along highways during the first few hours after sunrise, shortly before sunset, and shortly after a rain. During the summer they generally are in pairs but in the winter months are in flocks, and the pairs are distributed more widely than the flocks. Thus a highway census during the summer might record several doves within ten miles, whereas fifty miles of travel might be necessary during winter before the first flock would be observed. Highway censuses

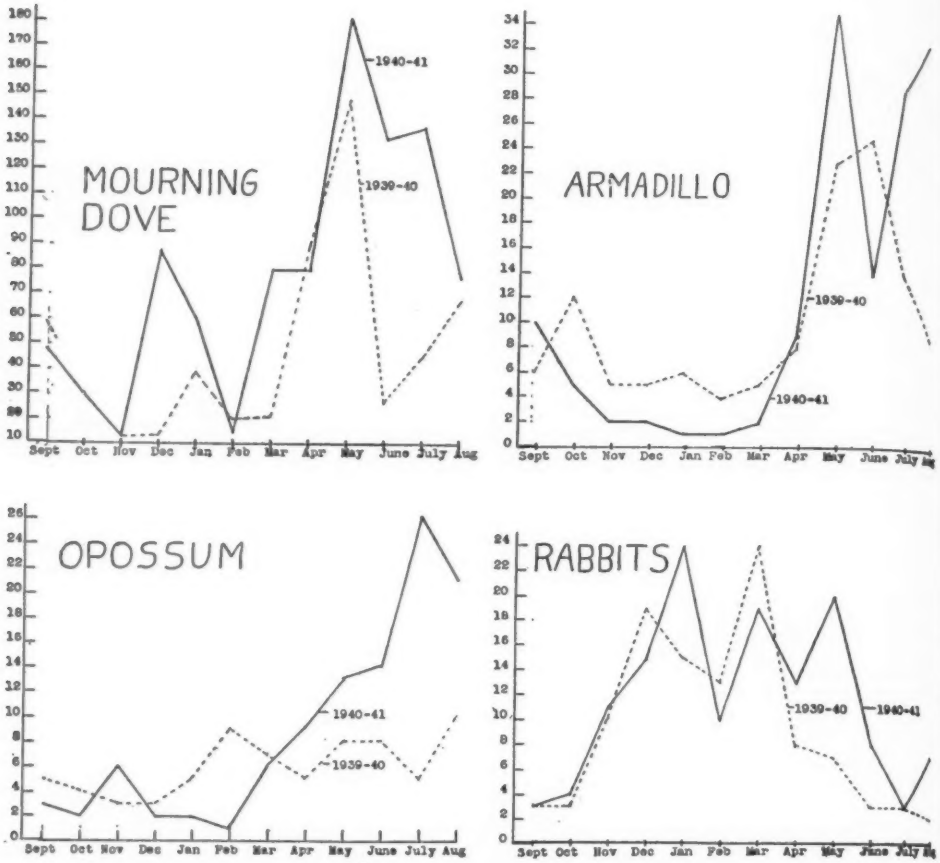

Fig. 1. Monthly censuses of animals on highways in eastern Texas, 1939–41. Mourning dove, all birds seen in censuses on 510 miles of road; armadillo, opossum, and rabbits, dead individuals seen on 2,000 miles of road.

therefore seem to be of little value for determining population density from one season to the next.

Highway counts may show the relative abundance of doves as between two or more major plant zones. In trips from the pineywoods of eastern Texas to the coastal plains, many more could be counted, consistently, along coastal highways than along those in the pine forests; but it is uncertain whether lack of roosting places on the plains forces the doves to roadside telephone wires. When travelling from pineywoods to blackland prairie, the counts were consistently higher along highways in the transitional scub oak between the pineywoods and blackland prairie, a difference that could not be ascribed to lack of roosting places. The indications are that highway counts will reveal relative population densities between major vegetative regions.

Notes on life history were garnered during the highway census. In eastern Texas doves begin to pair off early in

March, and the first flocks are seen late in August. Observations could of course have been gathered in any type of field work.

MORTALITY COUNTS ALONG HIGHWAYS

Coleman C. Newman

About 2,000 miles of highway were traversed each month for two years in Trinity, Angelina, and Polk counties, Texas, and records made of all dead mammals (except small rodents) seen along these roadways (Table 1). The resulting figures corroborate the conclusions of other persons who have made highway mortality counts—the toll is varied and large.

Several writers have attempted to demonstrate the enormity of highway deaths by calculating from counts the total possible mortality on the entire highway system of a county or state, or the nation; examples are those by Davis (3) for mammals and by Leedy (14) for pheasants. Attempts to deduce the average kill per mile have been made by many observers: Dickerson (5), Dreyer (6), Scott (22), Smith (23), and Starrett (24) for various species; Nichols and Raven (19) for skunks; Williams and Nelson (34) for rabbits; Sprague (26) for jack rabbits; and Russell and Amadon (21) and Stoner (28) for birds. Generally, however, authors simply have listed the numbers of animals found along certain strips of highway: Berg (1), Clark (2), Davis (4), Hadley (8), Hammond (10), Hein (11), Knobloch (12), Larson and Fox (13), Martin (17), Stoner (27), Stoner (30), Stoner (31), Warren (32), and Wilford and Wilford (33).

Can we deduce from such figures (Table 1) the relative abundance of several species, their relative vulnerability to traffic, or their relative mobility? Each question is negated by the other two. For instance, we cannot assume that the figures indicate the presence of the more armadillos than rabbits or opossums, because each of the other two may be less vulnerable to traffic or less apt to traverse the highways. Equal numbers of dogs and cats were killed during the two years, which may indicate equal numbers in the countryside for those years, but affords no proof, since one or the other of these domestic types may be more vulnerable to traffic. The figures tabulated afford some general impressions as to the relative abundance of the various mammals killed along highways, but do not constitute satisfactory scientific evidence.

TABLE 1.—NUMBERS OF DEAD ANIMALS OBSERVED ALONG TEXAS HIGHWAYS, 1939–41

Species	Sept. 1939–Sept. 1940	Sept. 1940–Sept. 1941	Totals
Armadillo	116	131	247
Rabbit	97	125	222
Opossum	60	93	153
Hog	48	28	76
Dog	38	35	73
Cat	31	42	73
Cow	2	7	9
Skunk	3	3	6
Fox	1	3	4
Mule	0	3	3
Raccoon	0	1	1
Squirrel	1	0	1
Goat	0	1	1

A further question arises as to whether highway mortality counts can be used in life history studies. Monthly records for the three species most often killed along the highways in the three counties under consideration have been assembled (Fig. 1). Highway counts

would be of some value in life history studies, if such records correlate with one or more of the following subjects: (1) mating activities, (2) increase in the population of inexperienced young, (3) temperature, (4) rainfall, (5) relative population densities, (6) availability of food, or (7) feeding habits. The records for each species may be examined in respect to these matters.

Armadillo. During both years mortality reached two peaks; both were higher in 1940 than in 1939; and from November to March the mortality of armadillos on highways was low. The abrupt rise of fatalities during May and June is correlated with the peak of the breeding season which occurs during those two months (Patterson, 20). Since the young generally are born in January and February it is also possible that immature and inexperienced armadillos provide for the rise in mortality. The low mortality during the winter months may result from temperature, rainfall, food availability, or other unknown factors. Armadillos are intolerant of cold weather and we infer that their inactivity during that period is responsible for the decline in highway mortality. Since the winter rains may make more food available by softening the ground and thus reduce the necessity for travel, the decline in mortality may be due to this reason. For the increased mortality during October of 1939 but not of 1940, and for that during July and August of 1941 but not of 1940, we have no explanation. The peaks of mortality were higher in 1941 than in 1940; these might have resulted from a gradual increase in population, a recovery in population since the drought of 1938, or greater numbers killed by the heavier traffic during army maneuvers in 1941.

Rabbits and Opossums. Among rabbits the outstanding facts are a low mortality during July, August, and September, a peak between November and January, a decline in February, and a rise during the spring months. There is no correlation between the fluctuations in mortality of opossums during 1940 and 1941.

Davis (3) kept daily records for a year of the mammals killed along six miles of highway in Brazos County, Texas. He found that cottontail mortality reached a peak during the winter, which agrees with our counts. This he attributed to food and cover being at a minimum during the winter and inducing more movements by the rabbits. We are inclined to agree with this assumption, but there may be other factors. Rabbits may wander less during the summer because of the hotter weather, or wander more during winter for physiological reasons of which we are ignorant. Beyond pointing out the possibilities, as Davis did, highway counts do not seem useful in life history studies of either rabbits or opossums.

What possible service can highway mortality counts then be to the research worker? We consider two uses made by various authors of particular value: one is so local in nature that a remedy is possible, and the other, made over a period of years, adds concrete information to the biologist's files.

The Michigan Conservation Department (18) recorded a kill of 60 deer along a 25-mile strip of highway in Michigan, to which the animals were attracted by salt strewn to reduce dust. Blocks of salt placed elsewhere to decoy the deer

away from the highway promptly reduced the mortality. Dickerson (5) recorded an unusually high mortality of kangaroo rats along one mile of highway in New Mexico; the rats were caught in a sticky bituminous oil spread along this strip of road. Larson and Fox (13) reported an unusual mortality of jackrabbits due to the unfortunate location of alfalfa haystacks along a particular portion of highway during dry weather. Warren (33) recorded instances of high mortality among prairie dogs where there were population concentrations on one side of the road; the animals were killed as they tried to return across the road to their holes. Williams and Nelson (34) counted 433 dead rabbits along six miles of highway but gave no cause for the unusual mortality. The foregoing are examples of mortality so unusual and local that remedies are possible.

Stoner (29, 30) has made observations on highway mortality for many years. By these he was able to record a gradual increase of the opossum in the northern states and to chart an extension of range by the porcupine in New York state. These records, made over a period of years, provided valuable data.

Carcasses found along highways have been put to various uses. Hamilton (9) examined highway victims in his studies on the breeding status of several species. Stoner (31) suggests that such specimens can be used for museum skins and to further the study of plumage and of food habits.

Other suggestions have been made by various authors. Some proved impractical in our work and others of only limited value. In this category are efforts to obtain indicies of distribution, population, lateral movement, and comparative abundance; to learn of the kinds of animals inhabiting a region; and to study the habits, reactions, and maintenance of numbers in relation to the highway menace which has become part of the experience of various animals.

Attempts to account for the rise and fall in mortality of various species found dead along highways, usually are made with the hope of suggesting remedies for such losses. Davis (3) suggests that opossum mortality is greatest in September and October because this species reaches its yearly population peak at that time and the young then are searching for individual territories. He also believes that cottontails in Texas are more subject to traffic accidents during January and Febuary because food then is at a minimum in the country and is most abundant along highways. He indicates furthermore that livestock grazing is heaviest in autumn and winter, thus bringing competition with wildlife and forcing the latter to feed along highways. He suggests that controlled grazing might be the remedy. Williams and Nelson (34) on the other hand found the mortality among rabbits in Idaho to be lower where there is overgrazing or cultivation, and greater where the countryside is heavily overgrown with sage brush. Sprague (26) attributes the higher mortality of jackrabbits along cultivated country to the fact that the rabbits are forced to use roadside vegetation. Berg (1) ascribes the peak mortality of skunks in western Texas between September and November to scarcity of food in the autumn which forces them to get

insects and carcasses from highways so that they may store fat for hibernation. Starrett (24) found that mortality in most species fluctuates with the seasons, but that of rabbits is on a maintained level. He concludes that most traffic accidents with small animals are unavoidable, but that many drivers need to be educated to avoid wildlife. Other authors simply list a number of possible causes for highway mishaps. Dickerson (5) in his comprehensive report believes that the following possibilities must be considered: relative density of animal populations in adjacent areas, land-use practices along highways, distance from road to escape cover, speed of car, blinding of mammals by headlights, and climatic conditions. Dreyer (6) also believes that temperature, humidity, precipitation, and the seasonal activities of animals are important. Knobloch (12) finds mortality to be smaller on gravel roads because of the slower traffic there than on concrete highways. Scott (22) lists weather, mannerisms of animals, food on cleared highways, and the character of the road as determining factors. Stoner (31) believes that the factors include: time of the year, temperature, and precipitation; ecological conditions bordering highways; locomotive ability, nocturnal proclivities, and feeding habits of animals; and the type of highway and number and speed of automobiles. Thus an array of variables must be considered and we conclude it is impossible to determine the causes of varying highway mortality or to suggest remedies except in certain local situations.

Remedies proposed for reducing highway mortality include: control grazing, graveling highway shoulders, culverts between lakes and swamps, removal of street lights to margins of roads to save toads and other insectivorous animals, and slower driving. Since highway mortality may result only in minor leakage in wildlife productivity, as amply demonstrated by Leopold (15), costly remedial measures are impractical.

CONCLUSIONS

The authors concur in the following conclusions as to highway censuses:

1. Counts of mourning doves during only two years will not reveal relative population densities from one season of the year to the next.

2. Such counts provide general impressions as to the relative abundance of doves between two major plant zones.

3. Highway mortality counts do not indicate the relative abundance, relative vulnerability to traffic, or relative mobility of one species as compared with another.

4. Such mortality counts are of little value in life history studies, but carcasses of animals dead on roads afford some kinds of information.

5. Highway mortality counts are of minor value for study of the distribution of species and lateral movement, population densities, and animal behavior.

6. Because of the many variables encountered, it is generally difficult or impossible to ascertain reasons for the rise and fall of mortality of species on highways; or to discover practical remedies for decreasing such mortality.

7. Such counts are of definite value in isolated instances of large local mortality, where the cause is readily apparent and remediable.

8. Such counts, over a period of

years are helpful in tracing extensions of range by some species.

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FOOD PREFERENCES OF MALLARDS ON THE CHIPPEWA NATIONAL FOREST, MINNESOTA

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A general investigation of waterfowl on the Chippewa National Forest was made by author from 1936 until 1940, and included censuses, cover utilization and nesting of the breeding ducks, their preferences as to autumn feeding grounds, and inventories of ducks shot by hunters. The censuses and the records of the ducks taken by hunters had shown where the birds were most abundant in summer and autumn. For effective management it was necessary to learn why the ducks preferred certain areas for nesting and for feeding. The studies here reported were begun in August, 1940 in an endeavor to answer the last question.

Local veteran hunters believe that wild rice (*Zizania aquatica*) is the most attractice duck food. Ranger Mel Cummings at Cass Lake, stated that this plant is the sole factor in determining whether a big flight of mallards will pass through the Chippewa area. This opinion extends also to the local crop of mallards and other puddle ducks; if the rice crop is poor or lacking, the ducks are thought to leave the area in quest of food elsewhere even before the hunting season opens. The Chippewa region includes three of the largest lakes in the state—Leech, Winnibigoshish, and Cass—and other small but famous hunting areas, hence a large part of the duck hunting territory of the state.

Martin and Uhler (1939) list wild rice as ninth in order of percentage of the total food in 7,998 ducks taken throughout the United States and Canada. In the eastern region it ranked third after all species of *Potamogeton* and *Polygonum*. Other research workers have found various species of *Potamogeton* and *Scirpus* to be more common in duck stomachs. In most cases, however, no attention was paid to local availability of the various foods where and when the ducks were procured.

Several factors affect the availability of duck food, not the least of which is hunting pressure. Most of the ducks used in past studies have been taken by hunters during the open hunting season. Ducks then are quickly "burned" out of favorite feeding grounds which are always frequented by heavy concentrations of hunters on the opening day. This is especially true of wild rice beds. When forced from such areas the birds retire to open waters or small inaccessible pot-holes where the available food may be much less palatable although acceptable. The birds often return to the better feeding grounds at night, but there is always more of the low quality food in their digestive tracts taken during their long daytime resting periods. Most studies of food habits therefore have been based upon ducks containing foods which they might not have eaten had they been allowed access to the better feeding grounds. Changes in water levels also control the availability of certain aquatic plants, either by rendering them inaccessible

to the "puddle ducks" or by preventing the seeds of such plants from maturing.

STUDY AREAS

The two objectives of the present study were to determine: (1) The actual food preferences of the mallard as correlated with the availability and abundance of food plants; and (2) The extent to which hunting pressure affects the foods actually taken. The mallard is by far the most important breeding duck on the Chippewa Forest area and also outranked all other species in hunters' bags from 1936 through 1940. The areas chosen for study, represent two of the more important feeding areas.

Mud Lake, of 1644 acres, is shallow, bordered by several hundred acres of sedge meadows, and dotted with many floating islands of cattail (*Typha latifolia*), soft-stemmed bulrush (*Scirpus validus*), bur-reed (*Sparganium eurycarpum* and *S. chlorocarpum*), reed (*Phragmites maximus*), sedges (*Carex* spp.) and others. In the open water areas there are pondweeds (*Potamogeton* spp.), wild rice, muskgrass (*Chara*), bushy pondweed (*Naias flexilis*), elodea (*Anacharis canadensis*), and others in lesser quantities. The lake is a veritable aquatic garden with representatives of most of the important aquatic food plants found on the Chippewa area.

The second area, the Third River Flowage, had been flooded since the autumn of 1937. Previous to that year, the flowage had been dry for some time, save for a narrow, meandering river channel. During the dry periods, the flowage was covered with a rank growth of sedges and had local patches of cattail and bur-reed. The flowages have been productive, both as to duck breeding and the take of ducks by hunters; they are temporary in nature but have a large influence on the Chippewa area during seasons when the rainfall is normal or above. The principal aquatic plants present include pondweeds (almost exclusively *Potamogeton strictifolius* and *P. zosteriformis*), coontail (*Ceratophyllum demersum*), sedges, star duckweed (*Lemna trisulca*), and bur-reed, with lesser amounts of other species. The area is important as a summer breeding and feeding ground and in autumn is primarily a resting area for waterfowl because of the many exposed mud flats and islands. Excepting for the river channel, the water varies in depth from several inches to 4 or 5 feet; the average is about 2 to 3 feet until late summer when the dam level is lowered and exposes the mud flats. Masses of aquatic vegetation then are deposited on these flats and form a thick mat completely covering the mud and sand.

FIELD PROCEDURE

The vegetation on the study areas was mapped during August and checked again during September, and notes were made as to the quantity of seeds produced by the various food plants. The emergent vegetation on Mud Lake had been mapped the previous winter with the help of CCC enrollees. The lake was gridironed with staff compass and chain and all islands of emergent vegetation mapped so that when the summer survey began it was comparatively easy to locate and map the beds of submergent species. The percentages of various aquatic plants present then were computed from the maps. Non-food species such as cattail,

horsetail (*Equisetum*), and water moss (*Drepanocladus*) were omitted. Other areas where ducks later were collected from hunters also were type-mapped during late September just before the hunting season

Mallards were shot during August and September by the author under permit, twelve being taken from each area every two weeks; the specimens were collected singly and each duck represented a different flock. Enough time elapsed between the collection of individuals to afford a good sample of the ducks feeding on the area during that period.

AVAILABILITY VS. USE OF FOOD

The following formula was used to determine food preference:

$$\text{Food Preference Rating} = \frac{\text{Per Cent of Use}}{\text{Per Cent of Abundance}}.$$

This formula had been developed during the previous winter, while the author was making some food habits studies with Marius Morse at the University of Minnesota. These ratings give an index to the actual food preferences of the ducks studied, provided the birds had been feeding entirely on the area studied, and unmolested. The greatest source of error in such a study occurs when ducks are driven from their favorite feeding grounds and forced to feed elsewhere.

MUD LAKE

PRE-HUNTING SEASON

From August 16 to September 16 91 per cent of the food of the mallards taken was wild rice together with seeds of bulrush, pondweeds, and bur-reeds (Table 1). The consumption of rice was quite consistent throughout the period; on August 16 it consisted mostly of pistillate flowers. Bulrush seed was eaten heavily in the first and second two-week periods (30%), but dropped in the last period (to 8.6%). The consumption of seeds of pondweed and bur-reed dropped in volume during early September but was higher before and after that period.

Potamogeton strictifolius had the highest food preference rating (3.41) during the pre-hunting season. If, however, the preference rating is calculated by two-week periods, that for August 16, when most of the ducks shot were still poor flyers and unable to leave the lake, the rating was down to 0.54. For September 4, it was 9.91 and for September 16 dropped again to 0.54.

The significance of this supposed change in preference is indicated clearly if the flight habits of the mallards from Mud Lake are considered, but no amount of laboratory study could explain the fluctuation. Actually there was no change in preference, but a change in availability because of disturbing factors. A definite local flyway exists between Winnibigoshish (Fig. 1) and Mud lakes. Mallards always have flown to the flowage areas around the former to rest when flushed from Mud Lake, whether by hunters or harvesters of wild rice. The height of the commercial ricing season was around September 4 and the presence of many Indians in the wild rice beds, from daylight until dark, prevented the ducks from feeding there during the daytime hours. The resting areas along the shore and flowage areas of Lake Winnibigoshish are of mud flats and shallow water where the birds can rest, undisturbed by man, and

TABLE 1.—PREFERENCE RATINGS OF FOOD IN 36 MALLARDS TAKEN IN PRE-HUNTING SEASON, AT MUD LAKE, MINNESOTA[a]

Species	*Relative abundance percentages*	*Use in percentages*	*Preference rating*
Potamogeton strictifolius	*1*	*3.4*	3.4
Zizania aquatica	*20*	*44.3*	2.3
Scirpus validus	*9*	*21.0*	2.3
Potamogeton natans[b]	*4*	*7.6*	1.9
Naias flexilis	*3*	*3.9*	1.3
Sparganium chlorocarpum	*4*	*4.1*	1.0
Scirpus fluviatilis	*2*	*2.1*	1.0
Sparganium eurycarpum	*5*	*4.2*	.8
Potamogeton pectinatus	*2*	*1.5*	.7
Potamogeton gramineus	*0.5*	*.3*	.6
Polygonum hydropiper	tr.	*.1*	medium
Eleocharis palustris	*1*	*.6*	.6
Carex spp.	*11*	*4.5*	.4
Polygonum lapathifolium	*1*	*.5*	.5
Ceratophyllum demersum[c]	*3*	*.6*	.2
Potamogeton zosteriformis	*3*	*.5*	.2
Potamogeton Richardsonii	*1*	*.1*	.1
Potamogeton amplifolius	*1*	tr.	low
Myriophyllum exalbescens	*2*	tr.	low
Prunus pennsylvanicum	tr.	*.5*	medium
Hippuris vulgaris	tr.	tr.	low
Polygonum natans	tr.	—	low
Sagittaria latifolia	tr.	—	low
Lemna trisulca	tr.	—	low
Lemna minor	tr.	—	low
Galium trifidum	tr.	—	low
Vallisneria Americana	*1*	—	low
Nymphaea odorata	*1*	—	low
Anacharis canadensis	*2*	—	low
Scirpus acutus	*2*	—	low
Chara spp.	*5*	—	low
Phragmites maximus	*8*	—	low
Nuphar variegatum	*6*	—	low
Total Animal Matter	—	*.1*	—

[a] Same method of tabulation used for each area studied.
[b] Seed crop exceptionally good.
[c] Seed crop poor.

feed at their leisure on the vast beds of *P. strictifolius*. The hard seed covering on this pondweed resists digestion for some time and hence much of the seed was present in the gizzards when the ducks returned to Mud Lake each evening. By September 16 commercial ricing had ceased and the ducks again could feed in the rice beds during daylight. This experience shows forcibly that in any food study it is necessary to know and correlate the local habits of the birds and their feeding conditions if food preferences are to be analyzed accurately.

Three other abundant species were close together for second position as to preference rating during the pre-hunting season period; these were, in order, wild rice, soft-stemmed bulrush, and *Potamogeton natans*. Bushy pondweed and *Sparganium chlorocarpum* were the only other species with a rating higher than 1; excluding *P. strictifolius*, the food preferences for the mallards of Mud Lake were clear cut and limited

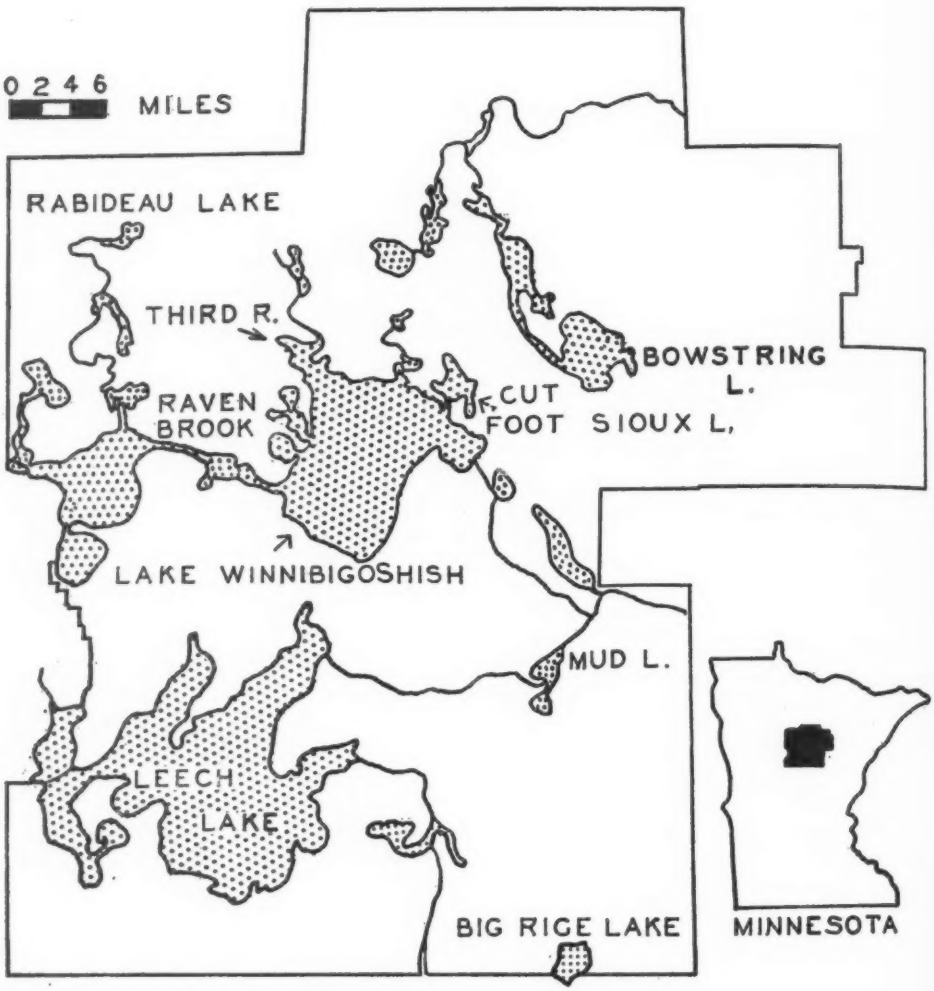

Fig. 1. Waters of the Chippewa National Forest.

to the five species mentioned. This is remarkable because there are over 35 different food plants in the lake.

From a management standpoint it is important also to know which species of aquatic plants apparently are not relished; these included *Chara*, reed, yellow water lily (*Nuphar variegatum*), and water milfoil. Perhaps the area taken up by such species should be made more productive by removing them and introducing species on the preferred list.

HUNTING SEASON

On preference rating alone, the smart-weed (*Polygonum lapathifolium*) was far the highest during the open hunting season. Its use was low during the closed season and it is not abundant

in the Mud Lake area; this would seem to indicate that the ducks obtained these seeds elsewhere and that the rating probably is not a true one for the area studied. Next in order of preference were bur-reed (*S. chlorocarpum*), *P. strictifolius*, wild rice, and water shield (*Brasenia Schreberii*). Bushy pondweed, soft-stemmed bulrush, and *P. natans* all ranked high in the prehunting season, but fell to below a rating of 1 during the hunting season. Possible reasons for this drop are that all three plants ripen early and produce seeds during the late summer and that the bulrush which grows in mud at the edge of the shore and of floating islands is more or less inaccessible to the ducks during daylight hours because these areas are favored hiding places for hunters. Consequently the ducks shy away from these and all similar areas where heavy cover might shield hunters.

It is reasonable to assume that stomachs from ducks taken during the prehunting period give a better index of the preference for certain foods. The ducks then are feeding in a comparatively "undisturbed" state, whereas those shot during the season are constantly being driven from one feeding area to another.

THIRD RIVER FLOWAGE

Third River is a very different type of aquatic community than Mud Lake. Water fluctuations result in an unstable condition and many of the better food plants are entirely absent, but the very nature of the area makes it an ideal resting ground. During the late summer and autumn, ducks find dried up mud flats and islands, plenty of sand and gravel, and several thousand acres of shallow feeding grounds abounding in *P. strictifolius*. Morning and evening flights to and from these flowages begin just as soon as the wild rice ripens in the nearby lakes. Being driven from these rice beds early in the day by commercial ricing, the waterfowl must spend long hours on the "flowage" areas, and therefore do more actual feeding on the latter than they would if allowed to remain on the rice beds for prolonged periods.

The mallards collected on August 15 were all "jump shot" and most of them obviously had been raised on the area. Again, on September 3, most of them were jump shot, although a few were shot overhead. On September 18, however, all but one or two of those taken were flying over and had just come from other areas, presumably the wild rice beds to the north. On all three dates the birds were collected during the forenoon, those on the last date before 8 A.M.

Considering the data by two-week periods we find that on August 15, before the rice had become ripe, 84 per cent of all food taken was *Potamogeton strictifolius* seed. Animal food amounted to another 4 per cent and wild rice only 0.25 per cent. On September 3 the rice was ripening but commercial harvesting was in full progress and the ducks were able to feed in the rice beds only after dark. *P. strictifolius* then comprised 78 per cent of the food taken, but rice was second with 13 per cent; animal food still was quite high in amount.

On September 18, however, all commercial ricing had ended. Rice actually was less abundant than before, by several hundred tons, but there was

more time for the ducks to feed. The consumption of rice by the mallards rose to 53 per cent and that of *P. strictifolius* was only 29 per cent. Two species of aquatic food plants thus made up nearly 87 per cent of all the food consumed by 37 mallards between August 15 and September 18, although 27 other species of food plants were present on the Third River area and many more on the surrounding lakes where the rice beds occur. Thus preferences on the Third River area prior to the hunting season definitely showed that wild rice was sought and that the mallards made regular flights to other areas for the express purpose of procuring this food. Plenty of other food was available in the areas where the wild rice beds occurred, but little was taken.

Both sago pondweed and soft-stemmed bulrush had high preference ratings, but this resulted from low availability rather than high use. The use was only about 3 per cent of total volume for each but the percentage found on the area was even less. Most of the seeds from these plants evidently were eaten while the ducks were in the rice beds. *P. strictifolius* was by far the most important single food taken, volume alone being considered. It occurred on over 30 per cent of the area and therefore was procured easily by resting ducks.

Food plants also abundant but little used were coontail, *Carex*, giant bur-reed, star duckweed, and *Potamogeton zosteriformis*. Lack of seed on coontail and *P. zosteriformis* no doubt accounts for failure to use these species as both had poor seed crops; this seems to be a common failing, especially of the former.

RAVEN BROOK FLOWAGE

Much of the Third River Flowage is a refuge and it was deemed inadvisable to take ducks there during the open hunting season. The Raven Brook Flowage lies just a mile south of Third River, and the two flowages are alike in appearance as to species of aquatic plants present. Most of the ducks which use Raven Brook for resting and feeding before the hunting season seek haven on the Third River Refuge during the shooting hours of the open season. A definite flyway exists between the two, and nearly all ducks collected from Raven Brook were shot as they came directly from the refuge.

Seventy-eight mallards from Raven Brook yielded a good basis to determine food preferences during the hunting season. Wild rice was far the highest in rating with no close competitor. *Potamogeton Richardsonii*, *P. pectinatus*, and *P. zosteriformis* followed with ratings of over 2, and *P. strictifolius*, soft-stemmed bulrush, and bur-reed (*S. chlorocarpum*) all rated over 1. Both Third River and Raven Brook contain much more *P. strictifolius* than any other food plant, but the rating of this species was considerably lower than those of several others. The latter doubtless came from the same areas as the wild rice.

The consumption of wild rice and pondweed was as follows:

	Percentage use	
	Potamogeton strictifolius	*Zizania aquatica*
October 1	28	50
October 2–3	27	31
October 5–6	67	11
Oct. 30–Nov. 6	75	5

The presence of so much rice in the 24 mallards taken on the opening day

proves that they had been feeding in the rice beds to the north on the previous day or night as had been their habit since the rice ripened. By the second or third day, however, the use dropped sharply, because the rice areas were becoming "burned out" by hunting and fewer ducks returned. By late October most mallards had given up the habit or "luxury" of feeding on wild rice and ate what they could get in the safer flowage areas. Further proof of this is seen in the increased consumption of *P. strictifolius*, which is just opposite to that for rice. This resulted from increased use of areas where the pondweed was so abundant. In other words, food preference became secondary to safety from the guns of hunters and a food of lower quality was suitable so long as the mallards could feed in comparative safety. Hence food preference studies based on ducks shot during the hunting season do not reflect the true preferences of the birds. These results indicate that, contrary to a general belief of hunters, ducks do not feed properly or satisfactorily during the night, at least not in the rice beds. This is a strong argument for refuges. Plants present in abundance but not used to any extent were sedges, giant bur-reed, water milfoil, and star duckweed.

Further analysis of the mallards from Third River and Raven Brook showed that those shot before the hunting season contained a greater volume of food than those taken during the season. The one exception was of ducks collected on October 1, the first day of the season, when the mallards still had food in their stomachs from the previous day's feeding.

There was plenty of evidence in the study from these two areas to prove the value of refuges close enough to good feeding areas so that ducks can feed properly and sufficiently. In any section of the country where hunting pressure is too great, the ducks either leave entirely or congregate in nearby potholes or open water areas where foods often low in palatability and possibly in nutritive value, make up the bulk of their diet.

RABIDEAU LAKE

This lake covers 720 acres, of which nearly two-thirds is open water. Wild rice and other emergents occur in the shallows along shore, with heavier concentrations in three shallow bays. Of the food in 40 mallards, *Sparganium chlorocarpum* with a rating of 5.96 was by far the highest; next in order were *Potamogeton Richardsonii*, *P. strictofolius*, and wild rice. Rice made up 44 per cent in volume of all food taken, hence was the most important. The high ratings for the first two species resulted from their low abundance rather than high use, and the mallards evidently obtained these foods elsewhere.

In volume used by periods, rice occurred in nearly the same percentage from October 6 to 10 as from October 1 to 5. This differs from the results at Raven Brook and seems to be a contradiction but can be explained easily by considering the character of Rabideau Lake. Hunting pressure there is low, except perhaps for the first day or two of the season. Mallards are less likely to shun rice beds if there is enough open water immediately adjacent for them to alight on. They do so at safe distances from cover which might conceal hunters, then look about, and later swim into the rice to feed if all is well.

Food plants abundant in Rabideau Lake but not taken by the mallards included coontail, sago pondweed, and sedges. The absence of sago in the stomachs is easily explained; the seed crop was good but the plants grew in water too deep for the "puddle" ducks to feed.

BIG RICE LAKE

From Big Rice Lake near Remer, Minnesota, 60 mallards provided a good check on the food habits of the area. The lake comprises 2,760 acres of water, none over four feet deep and most of it less than two feet. Much of the lake is covered with cattails, bur-reed, duck potato, and sedges. Wild rice comprised 20 per cent of the food plants and muskgrass (*Chara*) another 20 per cent. The beds of muskgrass on all open water areas were free of emergent vegetation. *Sparganium chlorocarpum* again had a high preference rating of 6.42, considerably higher than *Potamogeton natans*. Wild rice was third rating 2.49, but as at Rabideau Lake, formed nearly 50 per cent of the total food and was the main local attraction for mallards. *P. strictifolius* also had a high rating, but this and *P. natans* together made up only 2 per cent of the total vegetation in Big Rice Lake. The seed crops of both were poor, and most of these foods evidently were obtained elsewhere. Plants low in preference rating included muskgrass, duck potato, sedges, and yellow water lily.

OTHER AREAS

Data from 16 mallards collected at Big Cut Foot Sioux Lake, and of 17 from Leech Lake are included in "all area" totals.

MALLARD FOOD PREFERENCES

Twelve species of food plants which ranked "1" or higher in preference rating for at least one study area are shown in Table 2. They are arranged in the order of average values for all areas; this is not entirely satisfactory as a basis for comparison because those with "high" ratings cannot be included in the average. The "high" rating was assigned when the food in question was not found on the area studied. Thus, in most cases, if there was only one per cent or less of the plant on the area yet the volume consumed was great, the rating would be represented by a fairly large figure. If the same volume of food was consumed but none was available on the area an indefinite "high" rating necessarily would be assigned.

On the other hand, exceptionally high ratings such as 58 for wild rice obviously result from mallards feeding on areas other than the one studied; hence a true rating cannot be ascertained. The fact remains, however, that foods with exceptionally high ratings are so attractive that ducks will fly fairly long distances to obtain them.

Species which seemed to be preferred consistently in all areas included:

1. Wild rice (*Zizania aquatica*)
2. Bur-reed (*Sparganium chlorocarpum*)
3. *Potamogeton strictifolius*
4. *Potamogeton natans*
5. Soft-stemmed bulrush (*Scirpus validus*)

Others which varied from low to high in rating but generally were preferred included:

6. Water smartweed (*Polygonum*)
7. *Potamogeton Richardsonii*

8. Sago pondweed (*Potamogeton pectinatus*)
9. Bushy pondweed (*Naias flexilis*)
10. Watershield (*Brasenia Schreberii*)

Medium to low ratings for plants like bushy pondweed, sago pondweed, *Potamogeton Richardsonii, P. zosteriformis,* and *P. strictifolius,* and hard-stemmed bulrush generally result from the fact that these often grow in such deep water that mallards are unable to reach them. Thus the mallards did not appear to prefer bushy pondweed in the areas studied. On small lakes of the Chippewa Forest, only 6 to 24 inches deep, in which bushy pondweed occurs in profusion, the birds congregated in large flocks as soon as the seeds ripened. In feeding the plants were pulled up and stripped of their seed, after which large masses of stems and leaves drifted ashore.

To measure or map accurately the availability of a given food plant for the mallard, all plants in more than 18 inches of water should be excluded. This would be almost impossible, requiring many depth measurements and even then would be susceptible to two sources of error:

1. Many plants grow in deep water but their seeds are available at the surface for a period that varies with ripening conditions. At the time of mapping the seeds may be available but soon after may drop off and fall to the bottom.

2. Water levels are apt to change between the time of mapping and the collection of specimens of ducks, thus affecting records as to the availability of seeds.

The best that can be expected in a study such as that here reported is to obtain an indication of the species preferred. It is impossible to rate one species twice as high as another just because the calculated "preference" rating is twice as great.

TABLE 2.—MALLARD FOOD PREFERENCE RATINGS FOR THE MORE IMPORTANT FOOD PLANTS IN ALL AREAS STUDIED

Food plant	Mud Lake, pre-season	Mud Lake, hunting season	Third River	Raven Brook	Rabideau Lake	Big Rice Lake	Cut Foot Sioux Lake	Averages for all areas
Zizania aquatica	2.3	1.8	high	58.2	1.5	2.5	high	13.2
Sparganium chlorocarpum	1.0	4.5	.4	1.0	6.0	6.4	3.6	3.3
Polygonum lapathifolium	.4	7.6	.2	low	—	—	.6	2.2
Potamogeton strictifolius	3.4	2.4	2.1	1.5	1.8	1.7	.7	2.0
Potamogeton natans	2.2	.6	low	high	high	2.8	high	1.8
Potamogeton Richardsonii	.1	.7	.1	4.3	3.9	low	high	1.8
Potamogeton pectinatus	.7	.1	2.9	2.9	.2	.1	high	1.0
Scirpus validus	2.2	.7	2.9	1.5	.3	.1	.8	.9
Carex spp.	.4	1.4	.1	—	.7	.1	.2	.9
Potamogeton zosteriformis	.2	.8	low	1.0	.2	.6	high	.5
Naias flexilis	1.4	.1	.3	high	.2	.2	low	.4
Brasenia Schreberii	—	high	—	—	high	med.	low	med.

TABLE 3.—FOOD OF 306 MALLARDS FROM CHIPPEWA NATIONAL FOREST, AUTUMN, 1940

Species	*Times used*	*Volume in per cent*
Zizania aquatica	186	*35.5*
Potamogeton strictifolius	148	*22.8*
Sparganium chlorocarpum	145	*11.1*
Scirpus validus	70	*4.0*
Potamogeton natans	88	*3.4*
Potamogeton Richardsonii	40	*2.3*
Naias flexilis	39	*2.0*
Ceratophyllum demersum	40	*1.5*
Potamogeton pectinatus	31	*1.5*
Carex sp. (unidentified)	22	*1.4*
Potamogeton zosteriformis	52	*1.3*
Carex pseudo-cyperus	11	*1.0*
Scirpus acutus	31	*1.0*
Sparganium eurycarpum	24	*.9*
Polgonum lapathifolium	25	*.9*
Potamogeton foliosus	11	*.8*
Brasenia Schreberii	13	*.6*
Scirpus fluviatilis	18	*.5*
Potamogeton amplifolius	19	*.5*
Bidens sp.	3	*.5*
Polygonum coccineum	6	*.4*
Chara	2	*.3*
Myriophyllum exalbescens	16	*.2*
Lemna trisulca	2	*.2*
Potamogeton pusillus	4	*.2*
Potamogeton gramineus	8	*.1*
Vallisneria Americana	1	*.1*
Prunus pennsylvanicum	8	*.1*
Lysimachia sp.	1	*.1*
Nymphaea odorata	4	*.1*
Eleocharis palustris	2	*.1*
Nuphar variegatum	12	*.1*
Carex retrorsa	1	*.1*
Carex lacustris	3	*.1*
Carex cryptolepis	1	*.1*
Lemna minor	1	*.1*
Polygonum hydropiper	6	tr.
Polygonum natans	11	tr.
Anacharis canadensis	2	tr.
Sagittaria latifolia	1	tr.
Carex scoparia	2	tr.
Carex diandra	2	tr.
Galium trifidum	4	tr.
Phragmites maximus	1	tr.
Total plant food		*95.9*
Miscellaneous plant debris	8	*.6*
Total animal food		*3.5*
		100.0

To obtain composite ratings for the principal food plants on all of the areas, the plants listed in Table 2 were assigned numerical ratings: first place, 5; second place, 4; etc., to fifth place, 1. The combined results were as follows:

	Composite rating
Zizania aquatica	26
Sparganium chlorocarpum	18
Potamogeton strictifolius	17
Potamogeton Richardsonii	11
Potamogeton natans	9
Potamogeton pectinatus	8
Scirpus validus	7
Polygonum lapathifolium	5
Naias flexilis	1
Brasenia Schreberii	1

This method places wild rice in first place merely because it had a high preference rating on more areas than any other species, but the index probably is as good as any upon which to make comparisons.

The ten food species just listed were outstanding as to occurrence in the mallard stomachs; if *Carex* spp. and *Potamogeton zosteriformis* are included the list of principal food species is complete. Table 3 shows that, as to use alone, these 12 species are mostly at the top of the list, the exceptions being *Brasenia Schreberii* and *Polygonum lapathifolium* which are replaced by coontail and hard-stemmed bulrush. The abundance of the latter two plants together with the inaccessibility of their seeds, tends to lower their preference ratings.

The importance of hard-seeded plants such as *Potamogeton*, *Sparganium* and *Brasenia* is exaggerated by the fact that their seeds resist digestion longer than do those of rice, smartweed, bushy pondweed, and bulrush. In consequence, the former remain in the gizzards for extended periods and are found oftener and in greater quantities than the softer-coated seeds.

Another question is that of nutritive value. The food value of starchy seeds

like rice certainly is greater than that of seeds like those of potamogetons which are largely seed coat or shell. In the autumn, ducks need sufficient fattening foods to prepare them for the long flights south, hence starchy foods seem to be the most needed. Hard-coated seeds may serve other functions such as aid in the grinding of food when gravel is scarce; or perhaps the shells of such seeds contain large amounts of calcium or some other element necessary in the diet. Obviously there is need to determine the nutritive value of various duck foods so that we may know the actual value of those foods which ducks seem to prefer.

Lacking such data, however, it is obvious that certain foods are not palatable; even if nutritious they would be of no value to waterfowl. On the areas studied, mallards showed decided lack of appetite for muskgrass (*Chara*), duck potato, giant bur-reed, water milfoil, and both the white and yellow water lilies. Inaccessibility also enters into the picture for certain plants such as duck potato and the water lilies. Some of the above mentioned plant species are of value as cover and food for muskrats, but on areas to be managed for "puddle ducks" such plants should be discouraged in favor of those producing both food and cover. Coontail, while not a good seed producer, has a place in management because it serves as a "culture medium" for aquatic insects and other organisms upon which ducklings feed during the first few weeks of life. In brood census studies on the Chippewa Forest, lakes and streams containing vast beds of coontail proved to be favorite feeding grounds of ducklings. The latter often were observed swimming through the coontail and picking up the small aquatic animals which abounded there.

If only those mallards taken from Mud Lake and Third River previous to the hunting season are used as a basis for food preference ratings, we probably have more accurate criteria upon which to base conclusions. From these data the preferred foods, in decreasing order of importance, appear to be: *Zizania aquatica*, *Potamogeton strictifolius*, *Scirpus validus*, *Naias flexilis*, *Potamogeton pectinatus*, *Potamogeton natans*, *Sparganium chlorocarpum*. No other species ranked near these seven so that the pre-season preference seems to be quite clear cut.

This study seems to bear out the viewpoint expressed earlier that wild rice is the food of greatest preference for mallards on the Chippewa National Forest area. When feeding on rice is discouraged by commercial ricing or by hunting pressure, other foods may be eaten readily but rice, when available, is the main choice in the autumn.

Another emphatic conclusion relates to hunting pressure and its effect on duck food preferences. Such pressure is always heaviest on the better feeding areas because the ducks concentrate on those areas for some time previous to the opening day. The pressure is heaviest where the best food is most available, hence ducks on those areas are subjected to the most disturbance. As a consequence, after the first day or two, the volume of use of any duck food in a particular region is *inversely proportional to the hunting pressure* on the water areas where that food is available, rather than being proportional to the *abundance of the food itself*.

Actually the food is not available to the birds if hunting pressure is great enough to "burn" the birds out of the area. Therefore an analysis of duck foods taken from ducks during the hunting season merely reflects the availability of these foods as determined by hunting pressure and not necessarily by the preferences of the ducks themselves. Consequently, wild rice has not shown up well in volume of use or in food preference rating in many duck food studies. Wild rice beds are very easily "burned out" by hunters especially if hunting occurs too early or too late in the day. The ducks then may shun the rice beds entirely and resort to feeding on the areas of open water or in pot holes where pondweeds, bur-reeds, sedges and grasses are the only foods available.

The Chippewa National Forest contains several thousand acres of wild rice beds which produce hundreds of tons of seed during normal years. Rice is definitely the main factor in determining whether or not a big flight of mallards will spend part of the autumn season on this area.

DISPERSAL AND SURVIVAL OF GAME FARM BOBWHITE QUAIL IN NORTHCENTRAL OKLAHOMA

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State game departments and many commercial breeders and sportsmen are raising bobwhite quail (*Colinus virginianus*) to restock former ranges and to supplement natural reproduction. Practices in the artificial propagation of this species have been developed over a long period of experimentation and now are rather standardized and generally successful. The value of such operations, however, depends primarily upon the ability of released birds to adapt themselves to wild conditions, to reproduce, and to furnish sport for the hunter. This study was undertaken to determine the feasibility of stocking quail habitats in Oklahoma with artificially propagated bobwhite.

A study area of about 3,000 acres was chosen on the Lake Carl Blackwell Project, west of Stillwater, Payne County, that offered three distinct advantages: (1) an abundance of game farm bobwhite raised at the project game farm; (2) a block of 21,000 acres of rather continuous and homogeneous quail habitat; (3) better regulation of hunting and the other human activities that obscure and upset relationships between bobwhite and the natural factors in their environment on private land.

It is general practice for game farms to release young bobwhite when about eight weeks of age; 837 (79%) of the 1,064 birds were liberated when seven to nine weeks of age. To compare the survivals at different ages, 28 (3%) were released when 13 weeks old, and 199 (18%) as adults. In addition, 200

bobwhite seven weeks old and 357 eight weeks old were released on contiguous parts of the project as a check for more extensive movements.

Table 1 gives a chronological history of the releases. Four releases, totaling 427 birds, were made during May and June when it appeared that conditions were most favorable. To compare success at different seasons, three releases totaling 637 birds were made in the autumn.

In all cases, the bobwhites were put down in habitats known to furnish their necessary requirements. Ten to 20 birds were released together in each instance. They were encouraged to walk out of the shipping boxes rather than to flush and scatter widely. Most liberations were made in the morning

TABLE 1.—HISTORY OF GAME FARM BOBWHITE RELEASED ON THE LAKE CARL BLACKWELL PROJECT, PAYNE COUNTY, OKLAHOMA, 1939–42

Date of release	Number liberated	Age	Conditions when released	Estimated number that established ranges (summer) and autumn)	Estimated number that survived to hunting season (end of November)	Estimated number that survived to breeding season (April)
Sept. 13, 1939	437	8 weeks	Hot and dry; food and cover poor; high population of wild birds; conditions generally unfavorable; game farm birds suffered from heat	None	None	None
May 27, 1940	20	Adult	Moderate and damp; food and cover excellent; low population of wild birds; some releases had broken flight feathers and flew poorly	None(?)	None(?)	None
June 15, 1940	107	Adult	same	30 (A few nested successfully)	None	None
June 25, 1940	100	7 weeks	Environment favorable; wild population below carrying capacity; game farm birds in good condition	60	50	45
Oct. 18, 1940	100	9 weeks	same	30	25	15
Nov. 6, 1940	72 28	adults 13 weeks	Environment favorable; adults wing clipped, flew poorly; very unsuspicious	Few adults 10 young	At least 1 adult; 5 young	No adults; a few young (?)
June 28, 1941	200	8 weeks	Weather favorable; wild birds still below carrying capacity of range; game farm birds in good condition	100	10	8

during periods of mild weather to give the birds opportunity for becoming adjusted to their new environments when conditions appeared to be favorable. Each bird was marked with an aluminum leg band, serially numbered, and also with a colored celluloid leg band. The color of the latter indicated the portion of the area on which the bird was released. The birds were seldom found in situations where the bands could be observed readily and no attempt was made to use combinations of color bands that would distinguish individuals. Some 150 birds also were marked by colored chicken feathers tied into their tails. Unfortunately this technique, described by the Game Management Division of the University of Wisconsin (1937. An upland game bird banders manual. 12 pp.), was not successful because all of the feather markers apparently were lost within a few hours to two weeks.

TABLE 2.—DISPERSAL OF GAME FARM BOBWHITE AFTER LIBERATION

Age and number of records	*Distance of movement; average and extremes (yards)*
FIRST SIX WEEKS	
Adults, 39	462(25–2,500)
Juveniles, 151	152 (0–2,700)
SEVEN WEEKS TO SIX MONTHS	
Juveniles, 4	4,660[a](100–14,080)
SIX TO 14 MONTHS	
Juveniles, 11	1,960(900–3,960)
Totals 205	395(0–14,080)

[a] Too high, see text.

Three methods were employed to obtain information on the dispersal and survival of the released bobwhites: sight records, bands reported by hunters, and spring trapping. Aided by a bird dog, the planting sites and surrounding areas were censused intensively throughout the month or six weeks after each liberation. Colored bands and feathers occasionally were noted on flying birds, but most of the sight records were obtained from whistling cocks that permitted a close approach on the ground or from birds that flew into trees. It was seldom possible to see the bands on birds walking or running on the ground because of the dense surface vegetation. Continuous census work indicated that less than half of the bobwhite on an area could be located in one day; consequently it was impossible to obtain complete information on the dispersal and survival of the various plantings. Attempts to determine the causes of natural mortality were unsuccessful; remains of only six banded birds were found during the investigation. Part of the study area was opened to controlled hunting each autumn and 138 bobwhite were shot and examined for bands. In 1940 and 1941, information on 57 additional birds was obtained by spring trapping conducted by Ray S. Stonaker, Superintendent of the Lake Carl Blackwell Game Farm.

DISPERSAL OF GAME FARM BIRDS

The data on 205 accurate records are summarized in Table 2. The figures for the first six weeks are believed to be representative of normal movements for both adults and young. The average for the period from seven weeks to six months is undoubtedly too high, since the number of records is small and one individual of the four moved at least eight miles. Returns on 42 young shot

from plantings made all over the state showed an average travel of 2,550 yards or 1.45 miles. The average movement indicated for the first year is believed to be somewhat low. At times adults apparently moved out rapidly from the liberation sites. For example, a male released on June 15, 1940 moved two miles back to the game farm in three days and another male moved four-fifths of a mile in seven days. The available data suggest that the young tended to remain closer to the planting sites than did adults.

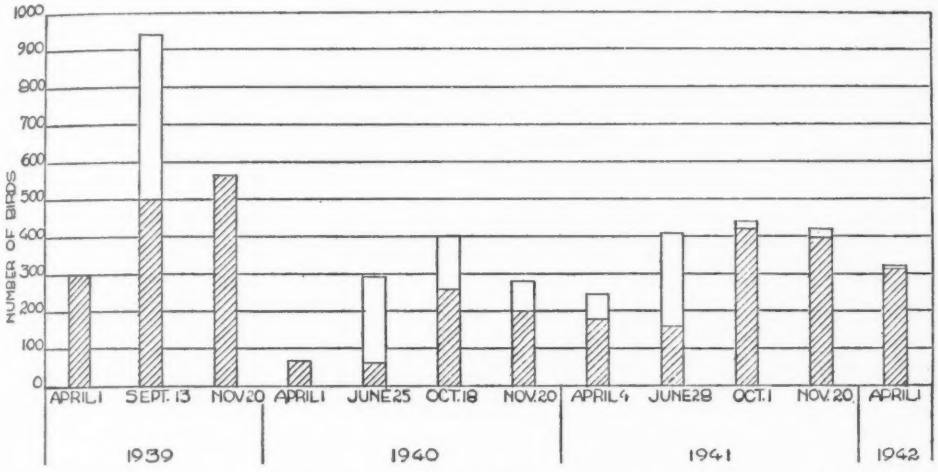

Fig. 1. Populations of bobwhite on the Lake Carl Blackwell Project, Payne County, Oklahoma, 1939–42. Diagonal ruling, wild birds; clear areas, game farm birds.

ESTABLISHMENT AND SURVIVAL

Game farm bobwhite showed wide variation in their ability to establish themselves and survive through the first year (Table 1). Only one adult was known to have been present during the hunting season and it represented a planting made only three weeks previously. Young birds, on the other hand, have shown some survival during every year except 1939, when environmental conditions were very unfavorable for bobwhite.

Table 3 summarizes the records on survival of the game farm birds; none was recovered from 71 shot on the study area in the autumn of 1939. The 1939 hunting results were substantiated by the fact that no banded birds were reported as shot around the project boundaries. Furthermore no banded birds were observed in the field until plantings were made in May 1940.

The populations of bobwhite (Fig. 1) were estimated from repeated counts

TABLE 3.—GAME FARM VS. WILD BOBWHITE RECORDED

Year and month	*Source of information*	*Game farm birds*	*Wild birds*
1939: Nov., Dec.	hunting	0	71
1940: Nov., Dec.	hunting	3	8
1941: Mar., Apr.	trapping	8	9
1941: Nov., Dec.	hunting	0	56
1942: Mar., Apr.	trapping	1	39
Totals		12	183

made on all coveys located during the autumn and winter, and from counts of whistling cocks during the spring and early summer. The figures on total populations obtained by these methods are believed to be accurate within 10 per cent. The proportion of game farm birds in the total population was determined by the specific records on birds obtained by hunting and trapping, correlated with sight records. These estimates may be subject to greater error.

Three of 11 bobwhite shot in the autumn of 1940 were game farm birds and this fact was used in a formula to estimate the number of game farm birds on the area:

$$\frac{3\,(\text{game farm birds shot})}{11(\text{game farm}+\text{wild birds shot})} = \frac{x(\text{game farm birds on area})}{277(\text{total estimated pop. on area})}$$

$$x = 76.$$

This figure checked closely with field observations made during the period when one-quarter to one-third of the birds seen in a number of coveys were banded. Using the same formula, a figure of 115 game farm birds was obtained from trapping results in the spring of 1941. However, seven of the eight banded birds were caught from one covey of eight and field observations indicated that about one-fourth of the birds in an average covey were banded. Consequently the number of game farm birds on the area was estimated to be one-quarter of the total population of 244, or 61. In a similar manner it was estimated that approximately 10 artificially propagated birds were present in the autumn of 1941 and 8 at the beginning of the 1942 breeding season.

MOVEMENTS OFF THE STUDY AREA

The data indicate that only a small percentage of the bobwhite released on the area moved off and became established on surrounding farms. Only three leg bands from the 1,064 birds liberated were turned in by hunters during the first or second hunting season following the date of release. These birds had moved approximately 0.75, 5, and 8 miles, respectively, from the original point of liberation. From 557 young liberated on other parts of the project during June in 1940 and 1941, seven bands were reported by hunters in the following 18 months; these were at distances of two to five miles from the points of release. Undoubtedly some bands were not turned in; also it is probable that some banded birds settled on farms bordering the project and were not shot. Nevertheless the fact that less than 1 per cent of the bands were reported indicates that the survival was probably not sufficient to supplement materially the population of wild birds.

ANALYSIS OF OBSERVATIONS

Errington and Hammerstrom (Iowa Agric. Exp. Station Research Bull. 201: 302–443, 1936) demonstrated that the winter carrying capacity of a given range apparently limits the maximum number of bobwhite it will support. The data from the present study agree with that concept. For example (Table 1) environmental conditions were very unfavorable in the fall of 1939, when the area was believed to have a higher population of wild bobwhites than the winter food supply could support. Consequently it was not surprising to find that the game farm stock released early

in the autumn failed to become established on the area and apparently soon died off completely. Wild breeding stock on the Project was depleted in January 1940 (Fig. 1) and the area became underpopulated. This situation was believed to account for the comparatively high degree of establishment and survival by game farm bobwhites from the summer of 1940 through that of 1941 (Table 1, Fig. 1). By the autumn of 1941, after two successful breeding seasons, the wild population again had reached the carrying capacity of the area. The addition of game farm stock in the summer of 1941 therefore did not result in any material increase in the total population for the autumn of 1941 and spring of 1942.

Restocking has two objectives as a management measure. Releases are important chiefly to supplement the wild breeding stock, particularly during years when the latter have been depleted seriously. In addition, quail artificially propagated furnish game for the hunter. The history of the releases of young birds indicated that during the year after a sharp decline in the wild bird population, up to 50 per cent of the game farm stock released in June were available for hunting and probably 45 per cent of them were present at the beginning of the following nesting season. On the other hand, when the wild bird population was normal the young game farm birds seemed unable to compete with the former and only a limited number survived. A small number of the adult females liberated at the beginning of the nesting season hatched broods and raised young. However, we do not have a single definite record of adult survival to the following hunting season, except for one male released only two weeks before the opening date.

Even during years of good survival the cost of the young farm-reared birds was high. Over a five-year period, the cost of raising and distributing young from the Lake Carl Blackwell Game Farm averaged about $1.00 per bird. If one-half of them survived to furnish hunting, the cost per bird shot was $2.00; if one-fourth survived to the following spring, the cost per breeder was $4.00. It is doubtful whether such high costs could be justified by state game departments and commercial breeders. The birds that moved off of the census area to take up ranges would increase the survival figures to some extent; yet only three of the 1,064 birds were reported by hunters, suggesting that such dispersal had no material effect upon the bobwhite populations of farms surrounding the project.

On quail hunting preserves where large revenues are obtained from the sale of hunting privileges, or on private holdings where the costs of production are of little consideration, restocking with game farm birds might be desirable following years when the wild population had been seriously depleted by overshooting or by unfavorable natural conditions.

SUMMARY

A field study on the dispersal and survival of 1,064 game farm bobwhite released on an area in northcentral Oklahoma yielded the following information:

1. Under unfavorable conditions for establishment, such as poor range conditions or a surplus of wild birds in the

area stocked, neither adults nor young established themselves.

2. When environmental conditions were favorable, both adults and young tended to take up ranges within a mile of the point of liberation; a few individuals dispersed rapidly and moved from two to eight miles during a period of a few days to several months.

3. Adult bobwhite liberated in the summer and autumn apparently were unable to cope successfully with conditions in the wild and did not provide stock for either hunting or breeding.

4. When environmental conditions were very favorable, it was estimated that as many as 50 per cent of the young furnished hunting in the late autumn and 45 per cent were available as breeding stock the following spring. A few survived the second summer.

5. Survival of the birds that moved off of the areas stocked was apparently so limited that they did not materially supplement the wild populations.

6. Heavy restocking with game farm birds appears to be costly and a rather futile method to increase bobwhite populations for either hunting or breeding stock.

THE BURSA OF FABRICIUS IN RING-NECKED PHEASANTS[1]

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The importance of determining the age of individuals composing a wild animal population has been explained by Leopold (1933), Gower (1939), Petrides (1942), Linduska (1943), and others. The separation of wild game birds into age classes during the autumn and winter, however, has been a problem until recently for those species in which the juveniles and adults bear similar plumages. The difficulty has resulted from failure to discover any purely objective characters which would distinguish juveniles from adults in a reliable percentage of the individuals examined.

Several characters have been proposed and tested as possible criteria of age; of these, the bursa of Fabricius has been studied considerably since being suggested by Gower (1939) as an indicator of age. The bursa (Fig. 3), which is peculiar to birds, is a dorsal diverticulum of the cloaca connecting to the cloaca by an orifice. Forbes (1877) and other European anatomists believed the organ to be present in all young individuals, but is not ordinarily found in adults excepting in some of the Ratitae (ostriches and rheas). Studies on the anatomy and histology of the bursa have been numerous. Jolly (1915), in

[1] Journal Paper No. 128, Purdue University Agricultural Experiment Station; the Division of Fish and Game, Indiana Department of Conservation, cooperated by supplying the pheasants used. Data from doctorate thesis at University of Wisconsin.

an exhaustive paper, described his own researches on the bursa and referred to many other papers, mostly by Europeans. He studied the anatomy and histology of the organ in a number of species. Calhoun (1933) reviewed the literature and studied the histology of the bursa along with the other parts of the digestive tract in the domestic fowl. The embryology of the organ has been studied by Boyden (1922).

Jolly (see Riddle 1928) stated that in chickens the maximum development of the bursa occurs at about 4 months of age, and that the beginning of its involution coincides with the appearance of sexual maturity. Riddle has interpreted this remark by Jolly to mean that the bursa begins to involute with the initiation of spermatogenesis. From the work by Riddle on doves, Gower on upland game birds, Hochbaum (1942) on waterfowl, and the data here presented, it is evident that in various kinds of birds the bursa begins involution long before the stage ordinarily referred to as sexual maturity.

On the basis of work by Jolly and previous investigators, the bursa was established as a lympho-epithelial organ, comparable to thymus tissue, and thought to be the site for formation of certain blood components. Riddle stated that in ring doves the bursa attained maximum size before gonad enlargement occurred. However, as soon as the bursa reached its maximum size, it immediately began to involute, and at the same time the testes and ovary began greatly increased rates of growth. Because of this behavior in relation to the gonads, it was assumed that the organ was somehow connected with the endocrine system, in addition to its hematopoietic function. This assumption was soon dispelled when Riddle and Tange (1928) reported that bursectomy did not change the rate of growth or the adult body weight in doves. Furthermore, bursectomy had no effect upon the age at which sexual maturity (determined by ovulation in females) was attained; hence, the bursa did not seem to have a vital function in doves. Although its function is still in doubt, the anatomy of the organ holds the attention of game management students because of its gross changes correlated with age. As Gower pointed out, "In using the bursa as an age character, only two factors need be considered: (1) its location and appearance, and (2) its span of existence." This author examined the ruffed grouse (*Bonasa u. umbellus*), sharp-tailed grouse (*Pedioecetes phasianellus campestris*), prairie chicken (*Tympanuchus cupido americanus*), spruce grouse (*Canachites canadensis canace*), ring-necked pheasant (*Phasianus colchicus torquatus*), Hungarian partridge (*Perdix perdix*), woodcock (*Philohela minor*), coot (*Fulica americana*), and several species of waterfowl. He noted that the bursa was relatively large in all (young) of these species during October, and stated that if it endured in wild birds as long as in chickens (about 8 months according to Jolly), it probably could be used as an age indicator through December and perhaps into January. Gower stated that use of the bursa for the aging of birds is limited (his method required the dissection of dead specimens) but since his report, other workers including Buss (1943), Linduska, and the writer have demonstrated that the presence or absence of the bursa is

rather easily discovered in live ring-necked pheasants. Mosby and Handley (1943) used the bursa as an age indicator in wild turkeys, but it is not clear whether or not they probed the bursa in live turkeys. In juvenile pheasants, the opening is so discrete in autumn and winter that a probe may be inserted (Pl. 6, *E*), and the depth of the bursa measured until the last month of its existence—early spring for some individuals. Hochbaum found examination of the bursa to be difficult in live waterfowl; in some cases he used a local anesthetic with success to relax the sphincter muscles about the vent.

Both Gower and Hochbaum mentioned the need for further studies to establish the time limits for usefulness of the bursa in various species. Accordingly, some objectives of the present study on pheasants were (1) to develop a simple method for measuring the depth of the bursa in live pheasants, (2) to investigate the relation of bursa growth and involution to other organs, and (3) to determine whether the bursa is as reliable in the spring as in autumn to differentiate adults and juveniles.

Studies were made on flocks of pheasants hatched in incubators and reared in confinement on a game farm, thus using birds of uniform and known ages. After bursa measurements were begun on a flock, the ration fed was not changed; age and nutrition, therefore, were ruled out as possible causes of variation. Wild and confined pheasants might differ as to the rates of growth and involution of the bursa, but the writer agrees with Linduska that any differences probably are insignificant. Otherwise a continuous series of bursa measurements from pheasants held under controlled conditions are valuable for comparison with similar data collected from birds whose ages and environments vary.

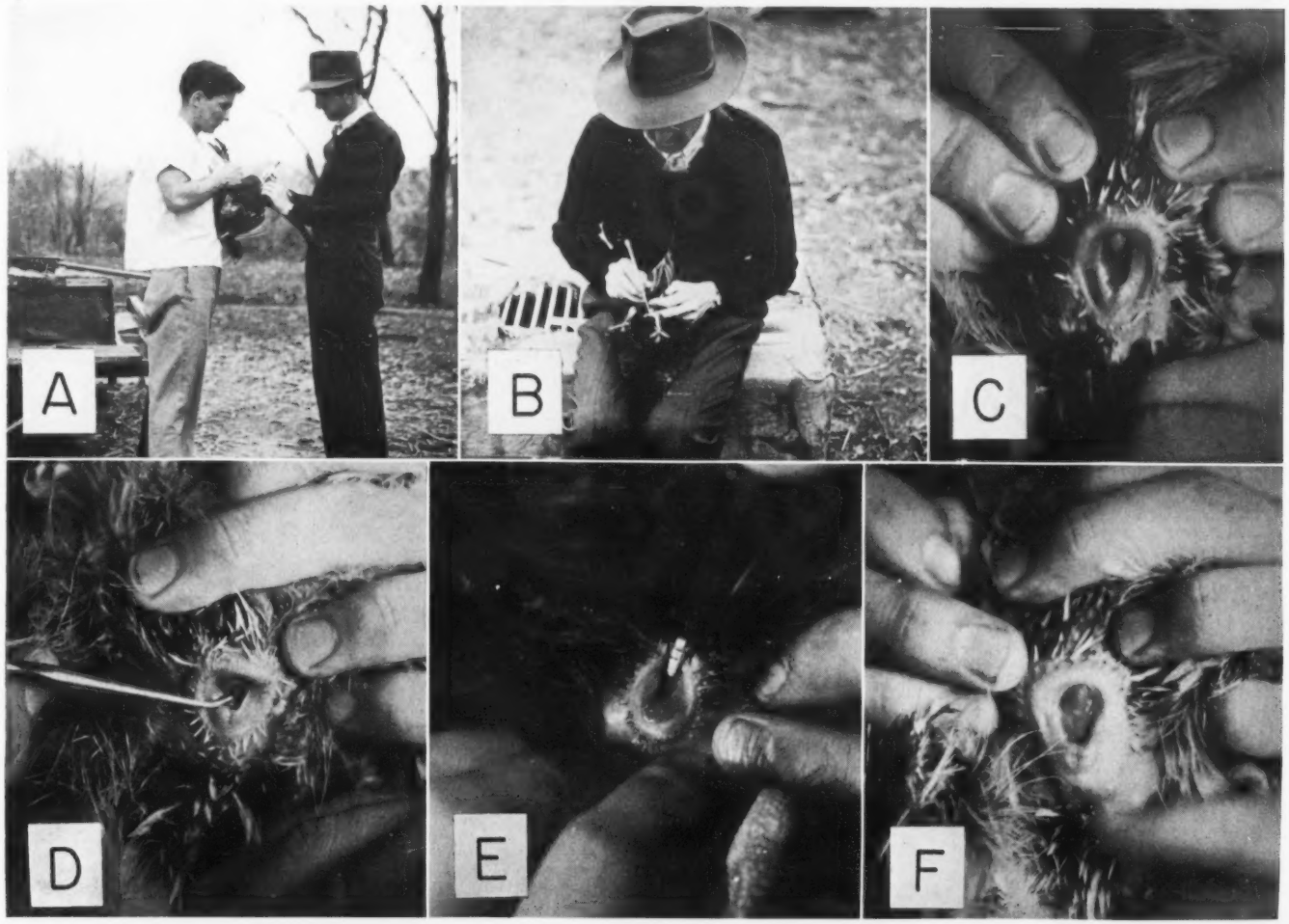
MEASURING THE DEPTH OF BURSA IN LIVE PHEASANTS

Three flocks of pheasants of different ages were used to obtain bursa measurements. These hatched on May 20, 1941, May 27, and July 5, 1942, respectively. The birds, confined in large outdoor holding pens, were wing-clipped to prevent injury or escape, and to facilitate periodic capture. They were marked with numbered metal bands to permit keeping records of individuals.

The bursae were measured at intervals of approximately five weeks. The 1941 birds were examined less frequently after they were a year old, but no persistent bursae (using the technique described later) could be found in adults. It was sometimes possible, however, to obtain measurements of 1 to 2 mm. in adults from a fold of the cloaca at the former site of the opening of the bursa.

Hochbaum had indicated previously (personal communications) that the presence or absence of the bursa could be determined in dead birds without dissection. He stretched the lips of the vent until the sphincter muscles were relaxed and then probed the dorsal wall of the cloaca for the opening of the bursa, using the quill of a wing feather. This technique he later reported (Hochbaum, 1942). Using the same method, the writer found that the presence of a bursa could be ascertained in live pheasants; development of this technique seems to have been coincident with similar work by Buss and Linduska.

To follow the rate of bursa involution



Studying the bursa of Fabricius in live ring-necked pheasants. *A*. Measuring the bursa when pheasant is held by an assistant. *B*. Method for one person to hold pheasant and measure the bursa. *C*. Cloaca of female; dark crescentic area is opening of bursa from which covering membrane is temporarily withdrawn. *D*. Use of metal probe to deflect membrane over opening of bursa. *E*. Glass scale inserted in bursa opening of male; bursa opens into dorsal side of cloaca. *F*. Female in which opening of bursa is

B. Method for one person to hold pheasant and measure the bursa. *C*. Cloaca of female; dark crescentic area is opening of bursa from which covering membrane is temporarily withdrawn. *D*. Use of metal probe to deflect membrane over opening of bursa. *E*. Glass scale inserted in bursa opening of male; bursa opens into dorsal side of cloaca. *F*. Female in which opening of bursa is

in live pheasants, some linear scale obviously was needed to measure the depth of the organ. Several devices were tried during the autumn of 1941, but none was quite satisfactory until an instrument of glass was designed (Fig. 1). A piece of 8 mm. pyrex glass tubing was heated and drawn to a smaller diameter at the heated point; about 35 mm. of the smaller diameter extended from the taper. The smaller end then was closed, annealed, and smoothed so that no foreign matter could enter the tube, and there was no roughness of the tip to injure cloacal tissues. A white celluloid millimeter scale, cut to fit inside the tube, then was introduced through the large open end. The rubber bulb of a medicine dropper was fitted over the open end to protect the inside of the tube from foreign matter and provide a convenient handle. Before the scale was placed within the tube, the annealed portion at the tip was determined to occupy 2 millimeters in length; accordingly, the same amount was removed from the end of the millimeter scale to compensate for this closure of the tube.

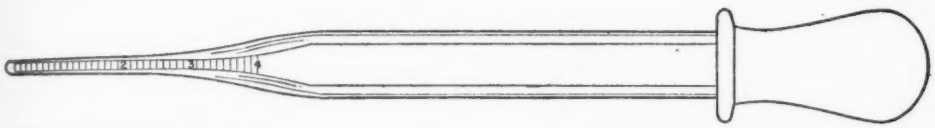


Fig. 1. Instrument for measuring depth of the bursa of Fabricius in live pheasants. Constructed of pyrex glass tubing, with millimeter scale from small celluloid ruler (numbered by centimeters), and rubber bulb from a medicine dropper to serve as handle.

This tool worked satisfactorily for pheasants. The tip of the scale was not more than 2 mm. in diameter, and in almost all pheasants examined, this was smaller than the opening of the bursa. The tip of the scale should be smaller than the bursa opening for the most accurate measurements. In earlier experiments a glass scale with a 3.5 mm. tip often completely occluded the opening, resulting in undesirable friction between the scale and opening. It was then difficult to judge when the tip of the scale had reached the end of the bursa cavity; observations on freshly excised bursae showed that stretching the bursa opening usually produced a proportionate shortening of the organ. Thus for birds smaller than pheasants, the diameter of the tip of the scale should not be larger than 2 mm. For larger birds, the length of the tapered part may need to be longer to measure deeper bursae.

For consistency, all measurements were made by the writer. Measurements usually were made with the help of an assistant to hold the birds, which expedited the work, but one person can examine the cloaca of a pheasant and measure the bursa without help.

In this study, the assistant held the bird firmly by both legs and one wing, with the tail of the bird toward the observer (Pl. 6, *A*). Sometimes the assistant held the bird by both legs in one hand, the bird being back down on his forearm, and its head held loosely between his elbow and body. With the head covered the pheasant remained quiet, and one hand of the assistant was free to help the observer spread the feathers about the vent. The person

using the scale works with his back to strong light for illuminating the inside of the cloaca and the bursa scale.

If the observer works alone on a few birds, as in trapping wild birds, examination of the cloaca and measurement of the bursa may be made without help. The observer sits upon anything handy or simply squats upon his heels. The wings of the pheasant are raised above its back and held, with the head and neck gripped lightly between the thighs of the worker (Pl. 6, *B*) If the pheasant struggles it will do so only momentarily, and both hands of the observer are free to make the cloacal examination

With or without help, the technique of using the scale for measuring the bursa is the same. (The following description assumes a right-handed person.) The thumb and index finger of the left hand grasp the dorsal lip of the vent or the feathers immediately next to it (Fig. 2, *X*), and this part of the vent is pulled toward the tail (direction of the arrow, Fig. 2). At the same time the other fingers deflect the feathers at the lower lip of the vent in the opposite direction, so that there is an unobstructed view of the cloaca with as much light as possible. The tension on the dorsal side of the vent reveals the inside of the posterior part of the cloaca (proctodeum) into which the bursa opens. Often the opening of the bursa is seen at once as an orifice in the dorsal

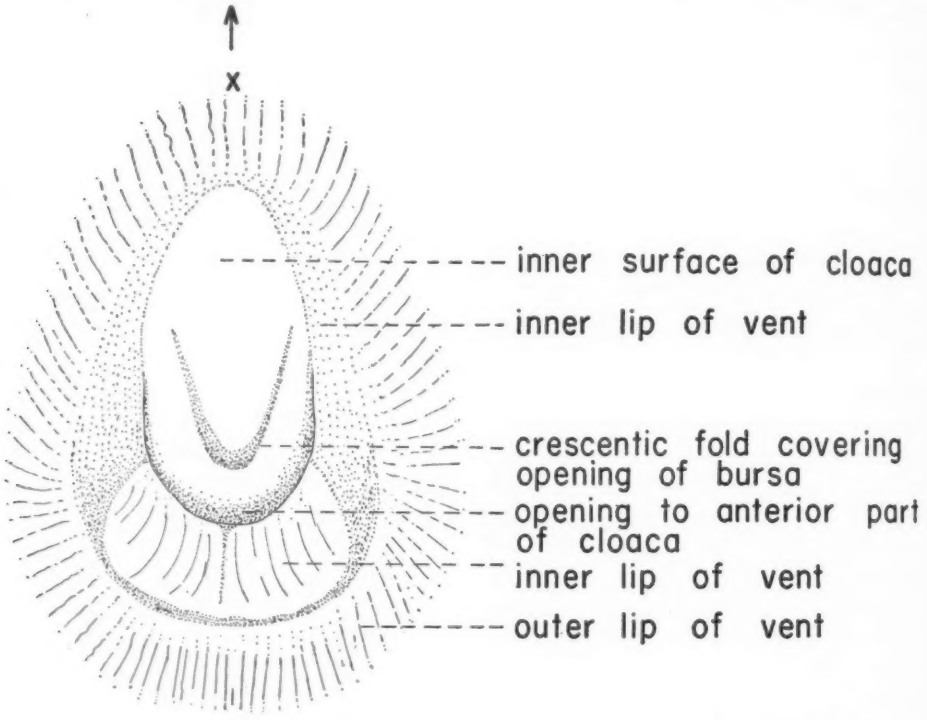

X
inner surface of cloaca
inner lip of vent
crescentic fold covering opening of bursa
opening to anterior part of cloaca
inner lip of vent
outer lip of vent

Fig. 2. Diagram of cloaca of ring-necked pheasant when dorsal part of the vent (X) is pulled in direction of the arrow.

wall of the cloaca (Pl. 6, *C*), but usually the opening is covered, although nevertheless marked, by a thin crescentic membrane on the dorsal cloacal wall (Pl. 6, *D*).

As soon as the opening of the bursa is found, the tip of the scale is inserted (Pl. 6, *E*) and gently pushed downward, with a rotary motion, causing the scale to become coated and lubricated with moisture from the inner surface of the cloaca and bursa. When the tip reaches the end of the bursa cavity, the resistance to easy progress of the scale is detected by the fingers. While the scale is gently held in place, the lips of the vent are allowed to relax as much as possible compatible with clear vision of the scale. This avoids much of the distortion of the bursa resulting when the vent is stretched. Where the edge of the bursa opening, or the membrane covering, crosses the scale, the reading is made to the nearest millimeter.

Certain difficulties often arise in locating the bursa opening or in measuring the depth of the bursa, even though the organ is known to be present. The membrane which often covers the opening to the bursa usually gapes conspicuously when the vent is opened (Pl. 6, *C*), but at other times this membrane adheres closely to the dorsal wall of the cloaca, making its crescentic outline difficult to see. If the observer has reason to believe that a bursa is present, he should explore the dorsal wall of the cloaca with the tip of the scale.

Occasionally a bird will come to hand with considerable urinary or fecal matter in the cloaca, which obscures the parts therein. Such a bird can be put aside for later examination.

A structure is often seen in the cloaca of a pheasant which presumably functions as a copulatory organ; it is termed the penis by Linduska. Burrows and Quinn (1937) describe in detail the copulatory organ of the domestic fowl and the turkey in both of which the organ consists of paired bodies of erectile tissue on the floor of the cloaca. (Until further study proves otherwise, it may be assumed that the anatomical features of the organ are essentially similar in all gallinaceous birds.) In pheasants the copulatory organ when relaxed appears as flaccid folds of the cloaca, and in this state it sometimes obscures the opening of the bursa when the vent is stretched. With careful manipulation of the parts, however, a bursa measurement usually can be obtained.

Probably the most difficult situation is encountered when the bursa is almost completely involuted. Then there is only a shallow crescent-shaped depression on the dorsal wall of the cloaca (Pl. 6, *F*), or this depression may be entirely absent; in the latter case the dorsal surface of the cloaca is vascular and uneven. Occasionally the membrane covering the opening may persist, permitting a measurement of 1 or 2 mm. A measurement of such proportions is obviously not a measure of bursa depth, since many dissections made during this study proved that no bursa existed when the surface of the cloaca was in this condition. Therefore, the data considered in the following discussion do not include bursa measurements of less than 3 mm. All smaller measurements were designated as 0 mm.

For a detailed description of the anatomy and histology of the bursa,

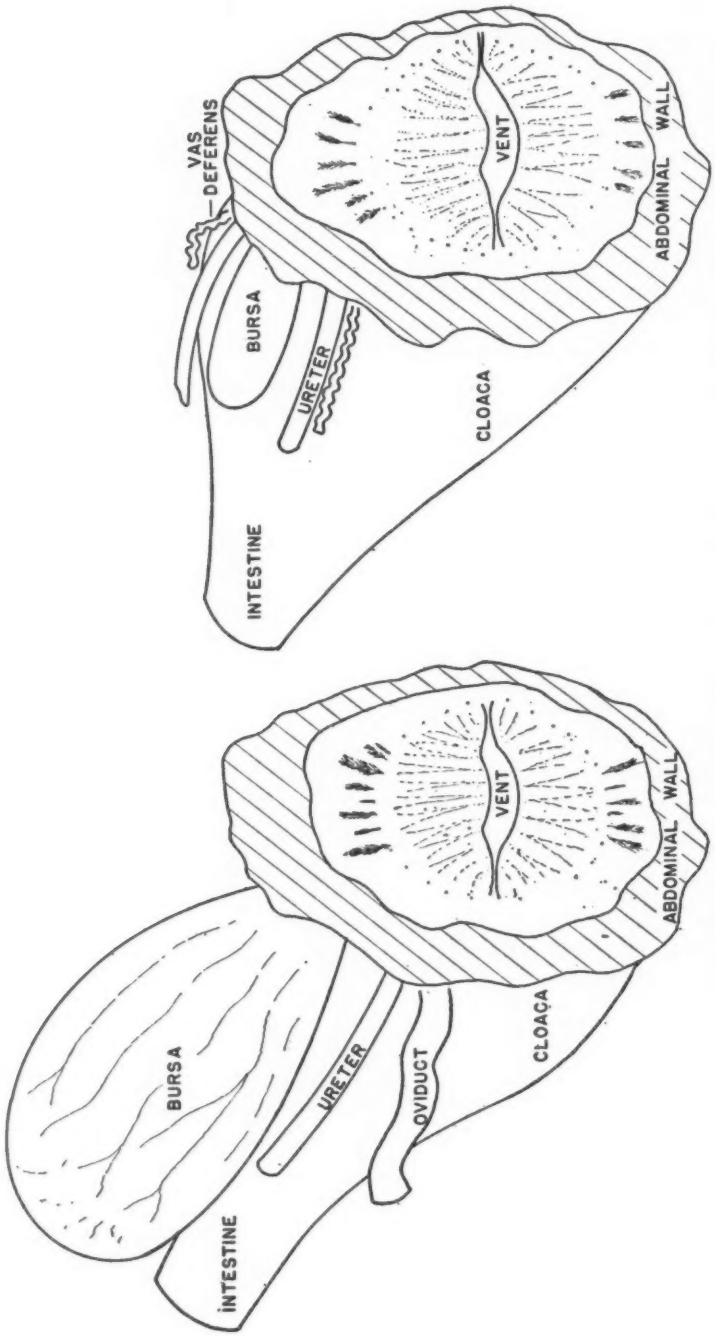


Fig. 3. Diagrams of excised cloaca and related parts in ring-necked pheasants. *Left.* Female, showing appearance of the juvenile bursa before involution. *Right.* Male, showing appearance of the involuting bursa.

the papers by Jolly (1915) and Calhoun (1933) may be consulted. For the purposes of this discussion it will suffice to say that in young pheasants the bursa is relatively large and thick-walled (Fig. 3). Generally this is true when the bursa is at least 15 mm. deep and the bird not more than 250 days old; but some individuals mature more or less rapidly than the average. In juveniles the opening of the bursa into the cloaca is usually conspicuous (Pl. 6, *C*). As the bird becomes older, the bursa grows progressively smaller in all its dimensions (some exceptions); the atrophied organ in a pheasant approaching sexual maturity looks not at all like the early juvenile structure. In the atrophying stage (Fig. 3) the opening of the bursa is still unobscured, and its cavity may be probed. Probing the shallow, thin-walled bursa must be done carefully with a blunt smooth instrument. Otherwise the delicate tissues composing the walls may be punctured, which apparently has no effect upon the welfare of the bird, but is likely to give an error in measurement.

INVOLUTION OF THE BURSA

The rate of bursa involution, measured by the technique described above, for three flocks of variously aged pheasants is shown in Figures 4 and 5. In all curves for both sexes there is a decided tendency for the average bursa depth to decrease to zero in late April, suggesting that the year or month of hatch does not influence the date when involution is complete. Linduska (personal communication) indicates that complete closure of the bursa in May hatched birds did not occur until the following May, and then in only 80 per cent of them. This difference in our results regarding the disappearance of the bursa probably reflects differences in measuring techniques.

The curves for the two years show different trends. On any one date from December to March, the average bursa depth of the 1942 hatch was from 1 to 10 mm. greater than that of the 1941 birds, suggesting that the year of hatching influences the average bursa depth on any given date. The July birds might reasonably be expected to have deeper bursae on any given date because they probably matured at a later date than the May birds of either year.

In pheasants hatched the same year, the younger birds have deeper bursae on a given date. Thus the average depth seems to be influenced by age in the autumn; but in the spring, flocks of different ages show approximately the same average bursa depth. This convergence of the bursa regression curves in the spring points to season, or some factor associated with season, as influencing the bursa depth at that time of year.

The involution of the bursa is continuous from September to April, but the rate of involution is much more rapid after January. This observation also was made by Buss on wild pheasants and suggests that some new influence on the bursa comes into play during January. Riddle found that in doves the bursa began involution simultaneously with that of the thymus and at the beginning of rapid growth of the gonads. Such a relationship between bursa and gonads also may exist in pheasants. Weight data for the thymus and gonads, and bursa measurements

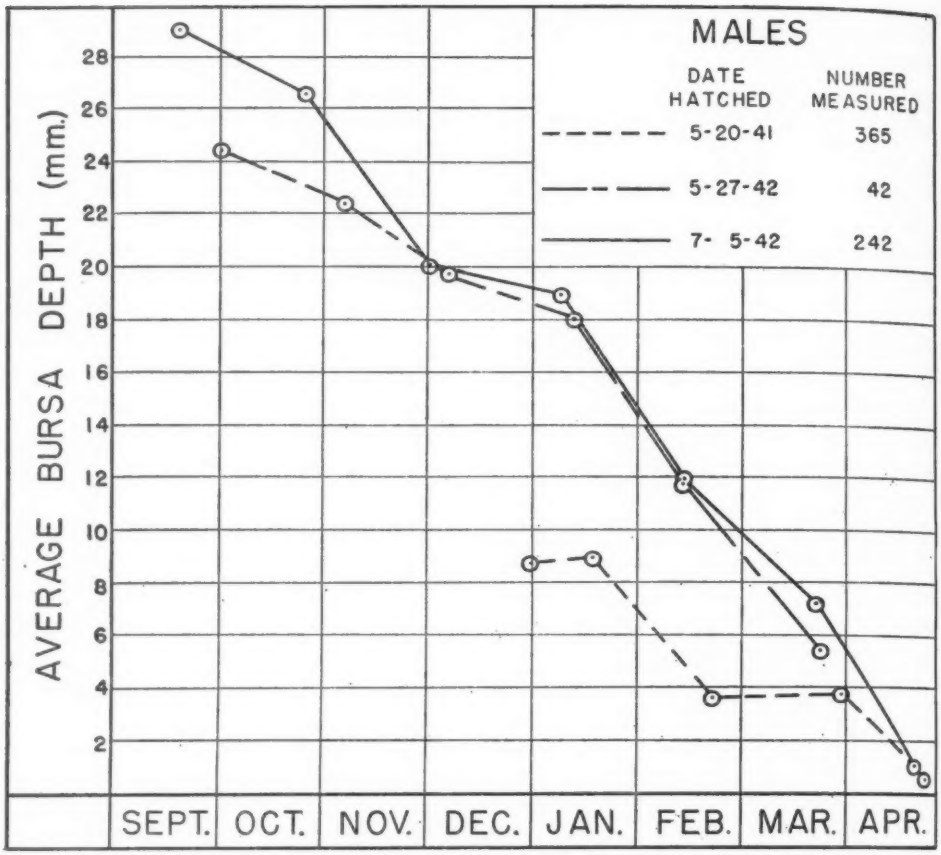


Fig. 4. Monthly average depth of bursa in male ring-necked pheasants, plotted to show the rate of bursa involution.

of the autopsied birds, were recorded for the 1941 flock (Kirkpatrick, 1943). The bursa and thymus began to involute at approximately the same time, when the pheasants were about 130 days old, simultaneously with a significant increase in weight of the testes (Kirkpatrick and Andrews, 1944); histological study of the testes from the autopsied birds showed spermatogenesis and formation of spermatozoa coincident with the initiation of involution in the bursa and thymus.

THE BURSA AS AN INDICATOR OF AGE

A bursa was found in all pheasants used in this study before the birds reached breeding age. In some individuals the organ did not disappear completely until late April. The writer found no cases of a persistent bursa in the flock of known-aged adults examined periodically. Therefore, on the basis of these observations, it appears that the presence of the bursa is a reliable indicator of the juvenile pheasant.

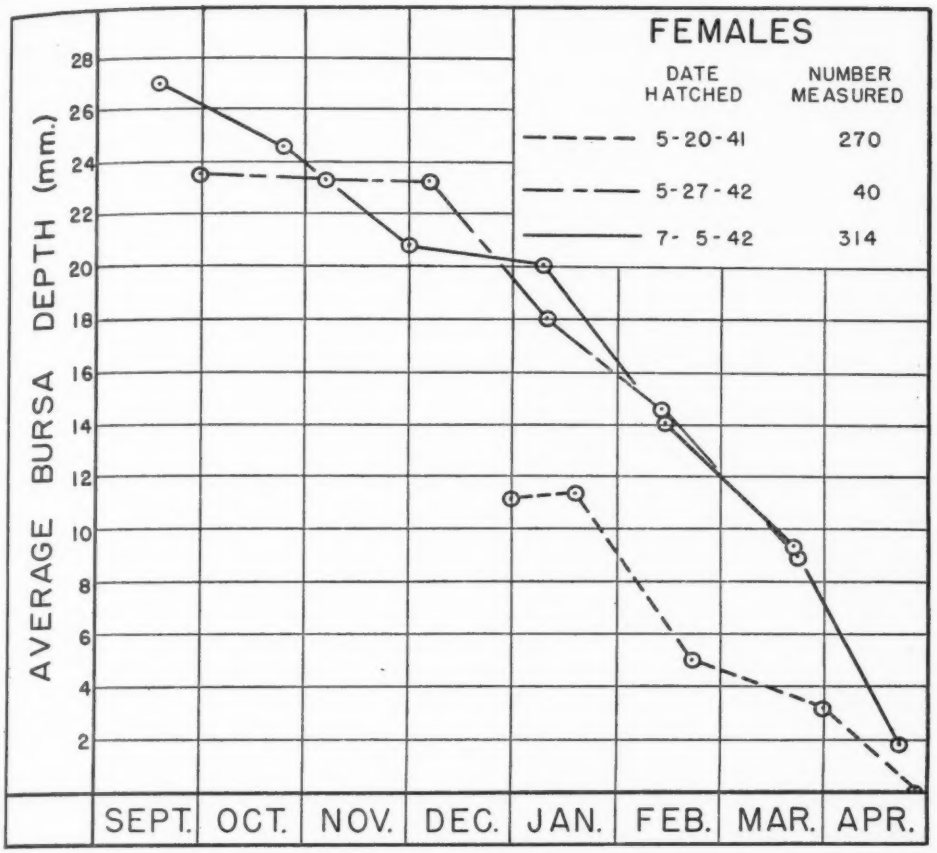


Fig. 5. Monthly average depth of bursa in female ring-necked pheasants, plotted to show the rate of bursa involution.

This conclusion is questionable, however, when applied to wild pheasants, since both Buss and Linduska report the finding of bursa remnants in a few adults. This would mean that the presence of a bursa would not be entirely dependable as a juvenile character at any time, but the error introduced by the presence of a bursa in adults would probably be small.

In some juveniles the bursa was completely regressed as early as January. Data collected from the pheasants hatched in 1941 agree with those of Buss in this observation. Thus a pheasant found after December with no bursa opening cannot be classified with certainty as either adult or juvenile. Other data from the 1942 birds agree with those of Linduska who thinks the bursa method of separating age classes is unreliable after January. Taken as a whole, however, the observations of the writer emphasize a point made earlier in the discussion—the later a pheasant is hatched, the deeper

the bursa will be on any given date up to spring. For example, the 1941 hatch came off on May 20. On January 18 following, the bursa in 10 per cent of the birds was recorded as of zero depth. On the other hand, of 176 birds hatched in July, 1942, measurements made on January 8 to 10, 1943, revealed no zero bursae. On the latter dates the average bursa depth was 18.2 mm. in males and 19.6 mm. in females. On February 14 only one zero bursa was found in 90 birds of the latter group. Hence, on the basis of observations made upon the 1942 birds, it seems reasonable to conclude that the presence or absence of the bursa is reliable through January as a criterion of age—but that ignores information from the 1941 birds and also the data reported by Buss. Therefore, while it appears that the date of hatching influences the time at which fully regressed bursae will first occur in a given flock of pheasants, the occurrence of zero bursae in the January measurements of one flock forces acceptance of December as the last month during which it is possible to separate juvenile pheasants from adults with high reliability. Indeed, if in subsequent work on large numbers of pheasants, zero bursae are found in December, this conclusion will have to be revised.

SUMMARY

1. The depth of the bursa of Fabricius in live ring-necked pheasants was measured by an instrument devised of glass tubing, a celluloid millimeter scale, and the rubber bulb of a medicine dropper.

2. To make the measurement: the dorsal lip of the vent is pulled posteriorly to expose the opening of the bursa within the cloaca; the scale is inserted into the bursa opening and gently rotated forward until its tip reaches the end of the cavity; and the depth of the bursa read where the edge of the bursa opening intersects the millimeter scale.

3. Involution of the bursa was studied and measured in three flocks of game-farm pheasants of known and different ages. The earliest measurements were made during September; involution proceeds from then until late April, when most of the bursae no longer can be measured. Curves for the average bursa depth of pheasants hatched in different years do not coincide during the winter months, suggesting that the year of hatching influences the average depth on any given date. In the autumn the younger pheasants of the same year have deeper bursae, indicating that hatching date is important as regards bursa depth. In the spring some factor associated with season may cause the completion of involution in all the pheasants by late April.

4. The bursa was found in all juvenile pheasants, but not in adults, hence its presence is a positive indicator of the juvenile bird. Some bursae are involuted completely by January 1 following hatching, hence December is the last month during which adults and juveniles can be differentiated by this method.

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MOURNING DOVE MANAGEMENT

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The mourning dove (*Zenaidura macroura*), like the upland plover, is a forgotten game bird. A glance through the Pittman-Robertson Quarterly will show how few states have projects on this bird as compared with quail, pheasants, or ducks. The four most popular game bird groups, according to data compiled by W. E. Crouch, are quail, pheasants, ducks and doves. In 1942 over eleven million doves were shot; this was one-half the number of quail shot, eleven-sixteenths the number of ducks, and eleven-fifteenths the number of pheasants. This great number of doves yielded proportionately less meat—one-third of that from quail, one-fourteenth as much as from pheasants, and one-fifteenth as much as from ducks. According to records compiled by K. McGrann, pheasants were hunted in 35 states, quail in 40 states, doves in 25 states, and ducks over the entire nation. It takes as many guns and as much shot to bag eleven million doves as for eleven million pheasants. This all means that the mourning dove is one of the major upland game birds.

With so much hunting of doves, a considerable income is derived from this species, but little is being done to perpetuate or manage the birds. As the record shows, Stoddard wrote a book on bobwhite, the Ohio Conservation Commission is producing a volume on the pheasant, there are many books and publications about ducks, but until the past five years, Mrs. M. M. Nice in Oklahoma had done the only comprehensive work on doves. There are now at least 15 states with research projects on pheasants. Ten or more have quail projects, and the U. S. Fish and Wildlife Service has a large personnel working with ducks. At the present writing, the only active dove project is in North Carolina. Pearson and Rosene in Alabama conducted a dove study from 1936 to about 1939, and the Game Commission of Iowa had a dove project from 1938 to 1941. Certainly a bird which furnishes as much sport as the ringnecked pheasant or the bobwhite quail deserves as much attention as those birds.

There is little knowledge as to the present status of the mourning dove. The American Ornithologists' Union Committee on Bird Protection found for 1942, "A very material shortage of the eastern form of the mourning dove." Publications from Alabama lack a clear statement of actual nesting densities, although Pearson does mention a few hundred nests on several thousand acres. Mark H. Taylor of North Carolina indicated (private correspondence) that four men found only 300 nests on several thousand acres. C. H. Kennedy reported 6,200 birds on 62,000 acres in Yakima Valley, Washington. Mrs. M. M. Nice in Oklahoma conducted roadside counts of the birds, but apparently made no effort to find all of the dove nests in any one locality. L. W. Wing reported six dove nests on 30 acres of broken land in Michigan. Apparently only H. E. McClure in Iowa has tried to estimate populations, finding as many as 1,500 nesting attempts on 220 acres in one season. Results of work in Nebraska (unpublished) show similar densities. From such sketchy evidence it seems that doves are much more numerous west of the Mississippi than in the eastern states.

The hunting regulations for the mourning dove in 25 states during 1942 varied as to length of season from 10 to 42 days; possession and bag limits were 10 birds in all. The A. O. U. Committee on Bird Protection recommends drastic reduction of both the length of season and the bag limit, especially in the east. The hunting season for mourning doves in 1942 was as follows: September 1 to 10, Idaho; September 1 to 15, Oregon; September 1 to 30, Illinois, Missouri; September 1 to October 12, Arizona, California, Kansas, Nevada, New Mexico, Oklahoma, North Texas; September 16 to 30, Minnesota; September 16 to October 27, rest of Texas; October 1 to 30, Tennessee; December 1 to 30, Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina.

The personnel of state conservation departments and of hunting organizations have differing viewpoints as to policy in the hunting of doves. In the South, there is a surplus to harvest; home-bred birds comprise only a small percentage of the wintering population,

and care is needed only to open the season after the local young have flown from the nests. By contrast, in the North the situation is quite different. There is only a small influx of birds from states to the north, but a rapid depletion of huntable birds through southward migration. The conservation and game departments are besieged by two groups. One says, "Let us have a shot at the birds. We raise them and the southern sportsman shoots them. Is that fair?" The other considers the dove a song bird of important economic value and wants no shooting. Hunters often favor a closed season, as was shown by replies to a questionnaire sent out in Nebraska during 1942, when 68.5 per cent favored a continued closed season. As to expenditure of state funds on research or surveys concerning the dove, most states assume that the bird is a migrant and investigations, therefore, should be made by the U. S. Fish and Wildlife Service.

Hunters disagree in opinions concerning the problem. Many northern hunters expend their energies on pheasants and consider the shooting of doves as they would the shooting of meadow larks. Southern hunters, however, assume an entirely different attitude, as stated by Joe Mears in *Sports Afield*. If we may judge by this and similar articles, the dove is simply a practice bird, to be shot at in preparation for duck hunting. It is to be hoped that the bird has more of a sporting chance in the eyes of southern hunters than such stories would connote.

To ornithologists, continued hunting of the mourning dove can only be justified if there is a shootable surplus and the species is in no danger of extirpation. The extinction of the passenger pigeon is a tragedy known to all, and a repetition of that catastrophe with our only remaining abundant dove is unthinkable. It is well to be reminded here that our other native species, the white-winged dove, is also in a precarious position. It is to be hoped that the combined efforts of sportsmen and conservationists in New Mexico, Arizona, and Texas will save the latter bird.

Judging by past actions, the personnel of the U. S. Fish and Wildlife Service has preferred to leave management of the dove to the separate states. The dove is migratory and the length of hunting season and of bag limits have been controlled through Federal regulations, but as the bird is reared in the various states that hunt it, more detailed research has been referred to the states. Hence, with the states expecting the Fish and Wildlife Service to act, and vice versa, but little has been done.

The new outlook: The idea is not exactly new, but it has come to the fore so far as to receive expression in the April 13, 1943 issue of *Look* magazine. With new and faster modes of travel being devised for war, the public will benefit from them after hostilities have ceased. Then, fast travel will probably be in the price range of nearly everyone. This will permit the hunter to travel cheaply and rapidly to the locality where the game he wants to hunt is most abundant—deer in Pennsylvania, Wisconsin or Colorado; quail or turkeys in Georgia or Missouri; pheasants in Nebraska or South Dakota; doves in the South, etc. In other words, this means that habitats best suited for the

production of game can be developed and game surpluses increased for harvesting by hunters from the whole nation.

DOVE MANAGEMENT

Dove management for the entire nation must no longer be attempted through the manipulation of state laws or local projects. The dove, like the ducks, is an international and interstate problem. It breeds from southern Canada to northern Mexico, and migrates throughout North America from Alaska to San Salvador. Activities of individual states cannot be expected to affect materially the entire dove population unless there is concerted and cooperative effort.

There should be no hunting north of the 37th parallel. Probably the division line should be along the southern border of Virginia, Kentucky, Missouri, Kansas, Colorado, and across Nevada and central California. All of the area north of this boundary should remain as a vast breeding range to maintain the species and to supply a shootable surplus. The reasons for this suggestion are seven-fold:

1. In these northern latitudes the dove is late in nesting. Over 20 per cent of the young do not leave the nests until after September 1, and in some areas, such as southern Iowa, two per cent remain in the nests after October 1. If the hunting season opens in September, one-fifth of the population is endangered.

2. An early migration accompanies this late breeding. Migration of young, and possibly of some adults, begins in late July and as rapidly as late young gain strength they, too, start south. The adults cease breeding in September and begin the southward movement as soon as they finish their last nesting attempts. Based upon roadside counts in Nebraska, there were 33 per cent as many doves seen in September as in July and August, and 0.5 per cent as many in October.

3. Some doves overwinter as far north as central Illinois, Iowa and Nebraska, but the population is small and would not serve hunting interests in any important degree.

4. Throughout the Midwest, doves nest in towns and about farmyards. Only 15 per cent of the population is produced in open fields or wooded areas away from such locations. As a result of this close association with man, laymen have an interest in the bird. It is considered as a songbird, and also is looked upon as the individual landowner's *own* bird. In speaking about doves, the layman commonly uses the personal pronoun—"my doves"—whereas in speaking of pheasants or ducks he says "the pheasants."

5. When the dove season is opened in such an area, hunters must look for the birds about farm groves and immediately come into friction with the farmer, for shooting near buildings arouses the ire of every farmer.

6. Besides its status as a song bird, the dove is beneficial in its food habits. Losses to farm crops such as result in the South from large aggregations of doves are rare in the North. According to Knappen (1938), Rosene (1939) and McClure (1943), the mourning dove eats only weed seeds or waste grain and, where populations are dense, the birds consume thousands of tons of weed seeds each year.

7. East of the Mississippi River, doves gather in great flocks through the states bordering the Gulf. This produces a shootable surplus. West of the Mississippi there are similar aggregations, but these scatter as the majority fly on to central and southern Mexico.

The probable explanation for greater numbers of doves west of the Mississippi River lies in the migration to Mexico. This is a practical demonstration of the method being suggested here: Iowa, Nebraska and South Dakota have for years been great breeding areas where the birds have not been molested, and hunting in Mexico has not been intense enough to deplete greatly the breeding stock for those states.

Management suggestions for these northern states in which the bird should be protected are as follows:

1. The dove is adaptable and will nest nearly everywhere but it prefers trees and shrubs. Continued planting of shelter belts in the West, replacing orchards in the Midwest, and planting evergreen windbreaks about farm buildings will offer additional nesting places.

2. Planting shade and fruit trees in towns to replace those that have died in recent dry years will further increase the nesting area.

3. In drier regions, the fencing off of small plots near overflowing windmill tanks will furnish drinking places; or the simple procedure of placing blocks of wood in open tanks will enable the birds to reach the water.

4. Since the dove is not specialized in its food habits and eats nearly any seed it can swallow, no special measures for its food need be taken in the North. In the South, food plots of dove weed, partridge pea, cow pea, or other small seeded plants occasionally may be advisable. But in the main, food is rarely a limiting factor for the dove.

In summary, mourning dove management should include no hunting of the bird in the northern half of its range and controlled hunting in its winter range. This is necessary because of its long breeding season and early migration, because the bird is considered a song bird in the North, and because it is beneficial in its food habits.

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HELMINTH INFECTIONS IN RELATION TO POPULATION FLUCTUATIONS IN SNOWSHOE HARES[1]

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Periodic fluctuations in animal populations have attracted the attention of biologists, astronomers, physicists, and philosophers, and are of vital interest to Indians, trappers, fishermen, and others depending on wild animals for sustenance and livelihood.

Some fluctuations are so marked and regular that the species concerned are termed cyclic; the best known are believed to follow a 10-year cycle. Those attracting most attention in North America are the snowshoe hare (*Lepus americanus*), ruffed grouse (*Bonasa umbellus*), and field mouse (*Microtus pennsylvanicus*); the last is believed to have a 4-year cycle.

In dealing with a living organism that has complex interrelations with its environment and with other species, no single explanation of these fluctuations obviously can be valid; yet it is seldom that effort has been made to weigh the relative importance of more than one factor. Various investigators have stressed sun spots or variations in solar activity, disease-producing organisms, or variations in climate and soil bacteria as the most important factors. The present study discusses parasitism and its role in animal fluctuations.

The writer has studied animal parasites in the gastro-intestinal tracts of about 1,000 snowshoe hares collected by

[1] Paper No. 2103 Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul. Prepared under joint cooperation by the Division of Entomology and Economic Zoology, University of Minnesota, and Pittman-Robertson Project 11-R, Minnesota Division of Game and Fish, Department of Conservation. W. A. Riley supervised the study and assisted in preparing the manuscript. Gustav Swanson also gave valuable aid in preparing the manuscript. R. G. Green provided most of the gastro-intestinal tracts used and gave access to his records. C. E. Mickel identified the dipterous larvae; the Minnesota Division of Game and Fish cooperated in supplying hares.

Dr. R. G. Green over almost one entire 10-year period (Sept. 1931–Dec. 30, 1940). The animals were taken during all seasons, and represented both sexes and all ages. This made possible a more extensive study of parasitic infections in a cyclic species than previously had been possible. The study included both the worm parasites and host reactions to their worm burdens.

REVIEW OF LITERATURE

Curtice (1892) published the first record of parasites of the snowshoe hare from near Washington, D. C. He recorded *Strongylus retortaeformis?*, *Trichocephalus unguiculatus*, *Taenia pectinata*, *Taenia serrata*, and *Monostomum* sp. Stiles and Hassall (1894) described as *Distoma tricolor* the trematodes which Curtice (1892) had identified provisionally as *Monostomum* sp. Seton and Hornaday (1909) examined hares that had died variously from septicemia produced by *Pyogenes aureus*, from generalized infections with tapeworm cysts, and from stomach worms (*Obeliscoides cuniculi*). Harkin (1927) reported finding four species of helminths from hares collected in Canada.

Christenson (1929) found a coenurus at the tip of the heart in a varying hare from Aurora, Minnesota. He fed the coenurus to a dog and 45 days later recovered tapeworms which he described as a new species (*Multiceps packii*). Skinker (1931) described *Passalurus nonanulatus* from snowshoe hares taken in Michigan and Washington. Schwartz and Alicata (1931a, 1931b) reported microfilariae, presumably of *Dirofilaria scapiceps*, from the blood of *Lepus washingtonii*. Boughton (1932) examined 420 hares collected in Manitoba from December 1930 to December 1931 and recovered 11 species of parasites. Of these he concluded that a hookworm (*Nematodirus triangularis*), a lung worm (*Synthetocaulus leporis*), and an *Eimeria* were capable of producing epizootics.

Alicata (1932) worked out the life history of the stomach worm, *Obeliscoides cuniculi*. Law (1933) found a heavy infestation of *Taenia pisiformis* among snowshoe hares in Ontario, and stated that a high peak of parasitism was reached in 1933. In 1935 J. F. Bell examined 75 hares collected in Minnesota between December 27, 1934, and August, 1935. In 1937 Green and Larson described a so-called shock disease believed to play a major role in causing fluctuations of hare populations. In 1938 they postulated that "a roundworm undergoing developmental stages in the lung tissue might be a source of a toxic agent which produces such derangement as we describe in shock disease."

MacLulich (1937) found 10 species in 105 hares from Ontario. Among these he listed *Protostrongylus leporis* from the duodenum; this is the correct name for the rabbit lung worm formerly called *Synthetocaulus leporis*,[2] which MacLulich discusses. Some other parasite of the duodenum apparently was incorrectly identified as *P. leporis;* this may have been a *lapsus calami*. Aldous (1937) analyzed the stomach contents of 54 Minnesota hares in 1931; 37 contained stomach worms (*Obeliscoides cuniculi*) in numbers from 20 to 250, averaging 99 per hare. Manweiler (1938) reported the first record of *Dirofilaria scapiceps* in the snowshoe hare from Minnesota specimens collected in 1935. Arnold

[2] Goble and Dougherty (1944) have now named this species *Protostrongylus boughtoni*.

(1938) published on the anoplocephaline cestodes of North American rabbits. Philip (1938) examined 172 hares collected in Alaska and recorded three species of helminths.

Highby (1938, 1943) studied the development of *Dirofilaria scapiceps* in wild Minnesota mosquitoes which had been allowed to feed on hares infected with the microfilariae of this species. Microfilariae were transmitted to domestic rabbits by the bite of infected mosquitoes and also by mechanical transfer to the scarified skin as evidenced by the recovery of adult *D. scapiceps* and microfilariae. Criddle (1938) listed the numbers of *Taenia pisiformis* cysts in hares collected in Manitoba from 1923 to 1935. Erickson (1940) reported the echinostome fluke (*Euparyphium melis*) in the stomach of a hare collected in Minnesota on July 9, 1936. In 1940, he reported the nematodes *Dermatoxys veligera* and *Nematodirus leporis* from the snowshoe hare. Penner (1939, 1940) experimentally infected snowshoe hares with the blood fluke (*Schistosomatium douthitti*) and with larvae of a tapeworm (*Cladotaenia circi*). Rozycki (1941) assembled host and distributional records on nematode parasites of North American rabbits.

MATERIAL AND METHODS

The gastro-intestinal tracts of 1,100 snowshoe hares were examined. The data on 147 were lacking or imperfect and their parasites were discarded. Of the remainder, 173 had been kept for varying periods in acre enclosures at Lake Alexander, Minnesota. The findings on them are considered separately from the 774 hares killed or found dead in the wild.

From the Minnesota Wildlife Disease Investigation at Lake Alexander, Dr. R. G. Green sent 788 (82.7%) of the hares used; 61 were collected in 10 other northern counties. Fifty-four were obtained from four counties in Wisconsin, and 34 were collected by Mr. Wallace Grange in Pine and Douglas counties, Minnesota and Wisconsin. Nine were shot in Manitoba by Dr. Green; five were obtained in Michigan, and the origin of two is unknown.

For the first six years (1931–36), when hares were increasing, 684 were available; 269 were obtained in 1937–40 when populations were low. The 953 examined comprised 391 males, 517 females, and 43 of unknown sex; 769 were adults, 179 immatures, and 5 of unknown age; 837 had complete gastro-intestinal tracts, 53 stomachs only, and 63 intestines only. The collections by months were as follows: January, 15; February, 32; March, 79; April, 79; May, 136; June, 101; July, 112; August, 93; September, 74; October, 83; November, 108; and December, 41.

Each gastro-intestinal tract was divided into its component parts; the contents were scraped into separate pans and washed in a sieve (400 meshes per cm.^{2}) which retained all worms. Material remaining in the sieve was placed by small portions in a black pan and water was added. Under an electric light, the worms were counted and then stored.

Adult cestodes were stained in borax carmine and Ehrlich's acid haematoxylin, then cleared in beechwood creosote. Larval cestodes were cleared in lacto-phenol before the rostellum was dissected out for study. Nematodes, also, were cleared in lacto-phenol. For

each hare examined, an autopsy card was prepared.

THE PARASITES

The internal parasites include three trematodes, nine cestodes, fourteen nematodes, one acanthocephalan, and four dipterous larvae. The last undoubtedly are accidental or spurious parasites. The following keys will serve to differentiate the known helminth parasites.

TREMATODA

1. Sexes separate; in blood vessels ..... *Schistosomatium douthitti*
   Hermaphroditic; not in blood vessels. (2)
2. Anterior end with collar of spines; total length about 1 mm... *Euparyphium melis*
   Anterior end without a spiny collar; total length about 1 mm... *Hasstilesia tricolor*

CESTODA

1. Larva encysted in muscles or internal organs, or free in body cavity or intestine ..... (2)
   Adult in intestines..... (5)
2. Larvae (cystericercus) free in intestine; rostellum of 38 hooks; large hooks 160–190μ long..... *Taenia sp.*
   Larva encysted in muscles or viscera, or free in body cavity..... (3)
3. Larva a fluid-filled vesicle (coenurus) containing many heads.. *Multiceps* spp. (Larvae of either *M. serialis* or *M. packii* not distinguishable.)
   Larva a bladder worm (cysticercus) with little fluid and only one head..... (4)
4. Large rostellar hooks less than 225μ long. Usually one head, but sometimes several due to budding..... *Cladotaenia circi*
   Large rostellar hooks 225–294μ long.... ..... *Taenia pisiformis*
5. One set of reproductive organs in each proglottid..... (6)
   Two sets of reproductive organs in each proglottid..... (7)
6. Rostellum with a circle of hooks; testes 3 per segment..... *Hymenolepis* sp.
   No hooks; testes many to each segment ..... *Schizotaenia americana*
7. Cirrus sac laterad of longitudinal excretory canal; testes confined to region between ovaries..... *Cittotaenia variabilis*
   Cirrus sac extending medial of longitudinal excretory canal; testes extending laterad beyond ovaries..... ..... *Cittotaenia pectinata americana*

NEMATODA

1. Probably no parasitic males; parasitic females not over 6 mm. long; uteri with 12–15 mature eggs..... ..... *Strongyloides papillosus*
   Parasitic males and females; latter with more than 12–15 eggs in uteri..... (2)
2. Esophagus a fine tube imbedded in column of glandular cells; anterior part of body filiform, posterior part thick and heavy; eggs lemon-shaped with opercular plugs..... *Trichuris leporis*
   Esophagus not a fine tube; anterior part of body not filiform; eggs without opercular plugs..... (3)
3. Bursa, if present, with rays..... (4)
   Bursa, if present, without rays..... (10)
4. Bursa not conspicuous; parasites of respiratory tract..... ..... *Protostrongylus boughtoni*
   Bursa conspicuous; parasites of gastrointestinal tract..... (5)
5. Spicules long and filiform, 0.65 to 1.7 mm..... (6)
   Spicules short (less than 0.5 mm. long) and stout, with crest and protuberances ..... (7)
6. Spicules 1.4 to 1.7 mm. long; lobes of bursa triangular; medio- and postero-lateral rays divergent..... ..... *Nematodirus triangularis*
   Spicules 0.65 to 1.05 mm.; lobes of bursa rounded; medio- and postero-lateral rays parallel..... *Nematodirus leporis*
7. Ventro-ventral and latero-ventral rays approximating at their tips; spicules cleft distally ending in two barbed processes; gubernaculum absent..... ..... *Obeliscoides cuniculi*
   Ventro-ventral and latero-ventral rays not approximating at tips; spicules not not cleft distally; gubernaculum present ..... (8)

8. Spicules 175 to 190μ, not similar; distal end of right spicules smooth, of left spicule serrated; anus to tip of tail of female 850μ to 1 mm. . . . . *Trichostrongylus calcaratus*
   Spicules less than 175μ. . . . . (9)
9. Spicules 130 to 155μ, distal ends with two blunt recurved hooks; anus to tip of tail of female 140 to 165μ. . . . . *Trichostrongylus affinis*
   Distal ends of spicules without blunt, recurved hooks; anus to tip of tail of female less than 140μ. . . . . *Trichostrongylus retortaeformis*
10. Esophagus not dilated posteriorly; parasites of leg joints. . . *Dirofilaria scapiceps*
    Esophagus dilated posteriorly into a bulb; parasites of intestinal tract. . . (11)
11. Posterior end of male short and blunt, with row of transverse comb-like crests on ventral surface; bulb not separated from rest of esophagus by constriction. . . . . *Dermatoxys veligera*
    Posterior end of male long and pointed; no comb-like crests; bulb separated from rest of esophagus by constriction. . (12)
12. Gubernaculum present. . . . . *Wellcomia evoluta*
    Gubernaculum absent. . . . . (13)
13. Tail of old females with circular cuticular thickenings; males with more than two pairs of circum-anal papillae. . . . . *Passalurus ambiguus*
    Tail of old females without cuticular thickenings; males with two pairs of circum-anal papillae. . . . . *Passalurus nonanulatus*

The four species of dipterous larvae found were *Fannia scalaris, Aphiochaeta xanthina, Sarcophaga* sp., and a schizophoran.

PRINCIPAL HELMINTHS AND THEIR FLUCTUATIONS

Five nematodes and one cestode of the 19 species recovered are considered significant in producing mortality: a stomach worm (*Obeliscoides cuniculi*), intestinal trichostrongylids (*Trichostrongylus calcaratus, T. affinis,* and *Nematodirus triangularis*), a pinworm (*Passalurus nonanulatus*), and a tapeworm (larva of *Taenia pisiformis*). A lungworm (*Protostrongylus boughtoni*), not recovered by the writer, is discussed briefly because of its importance in relation to mortality.

The incidence of the five nematodes over the ten-year period followed the same course with minor variations. The incidence of *T. pisiformis* was somewhat different, perhaps because the species requires two hosts to complete its life cycle.

Infections by the five nematodes during 1931–33 were comparatively low. In 1932 the incidence of trichostrongylids and of the pinworm were higher than in 1931 or 1933. Climatological data do not show that temperature and precipitation were more favorable for development of helminth ova in 1932 than in other years. The mean annual temperature and total precipitation were fairly uniform over the 10-year period and probably did not influence parasitism.

The infections by the five nematodes progressed fairly uniformly as hare populations increased until a peak of infection in 1935–36, when a precipitous decline in hares at Lake Alexander began. The percentage of infections remained high in 1937–40 but began to decline from the 1935–36 peak. In 1939–40 there was a slight increase in intestinal trichostrongylids. Hare populations continued to decline in 1935–38 and when the low point was reached in 1937–38, hares were difficult to obtain.

The percentage of infection with *T. pisiformis* reached a peak in 1936–37, but there was neither a gradual build-up

previously nor a gradual decline thereafter. The infection varied only about 10 per cent each year save in 1937 when it was 30 per cent from the average.

The infection by *O. cuniculi* was low from 1931–33 when hare populations were increasing, and a peak of infection was reached in 1935 when hares attained their greatest density and the die-off began (compare Figs. 1 and 2).

The rate of parasitism varied through the year. The heaviest infections by most parasites occurred in late winter and early spring. The average number per host varied for the different parasitic species and did not necessarily occur when the greatest percentage of hares was infected. Some factors that determine the percentage of infection and average number of worms are temperature, precipitation, type of soil, abundance and age of hares, and the level of immunity at any particular period.

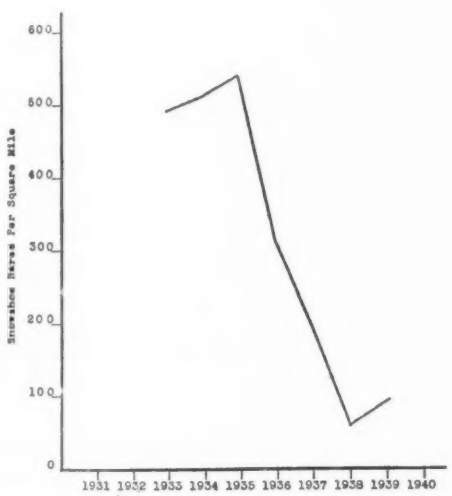


Fig. 1. Population of snowshoe hares at Lake Alexander, Minnesota (after Green and Evans).

The greatest infection by four nematodes occurred in late winter and early spring (Fig. 4), then dropped markedly in summer and autumn, probably indicating development of an immunity

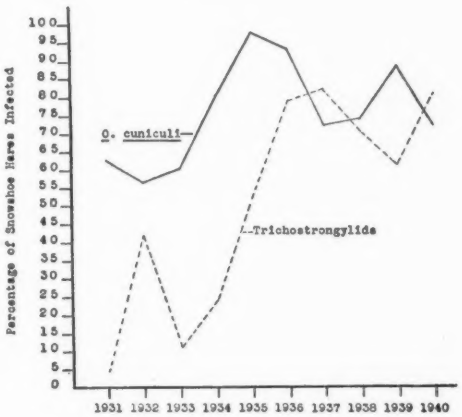


Fig. 2. Yearly variations in the percentage of snowshoe hares infected by *Obeliscoides cuniculi* and trichostrongylids (*T. calcaratus*, *T. affinis*, and *N. triangularis*).

similar to that found by Stoll (1932) and Sarles (1932). The percentage of hosts infected by stomach worms declined more slowly during the summer and autumn than in those infected with trichostrongylids, probably because of a lesser degree of immunity against stomach worms. The heaviest burdens of *O. cuniculi* and trichostrongylids occurred in March, May, July, and September. Both *O. cuniculi* and *T. calcaratus* require about one month to complete their life cycles, as probably do *T. affinis* and *N. triangularis*.

As to the host animals, some ecologists believe that more females than males are lost at the die-off in cyclic species, intimating that the former are more susceptible to decimating factors,

No differences were noted in the percentage infections as to the sex of hares by the stomach worm, trichostrongylids, or *Taenia pisiformis*. The total infection of 325 males by 16 species of parasites was 88.9 per cent and of 417 females, 90.2 per cent.

Immature animals, according to some authors, are more susceptible to parasitism than adults. More adult than immature hares, however, were infected by *O. cuniculi*, *T. calcaratus*, and *N. triangularis*. Of the important parasites only *T. affinis* occurred more frequently in immature animals (35%) than in adults (31%). The percentage of adults infected by stomach worms and trichostronglyids and the average number of worms per infected adult was much greater than among immature animals, but only 57 wild-caught immatures were available as compared to

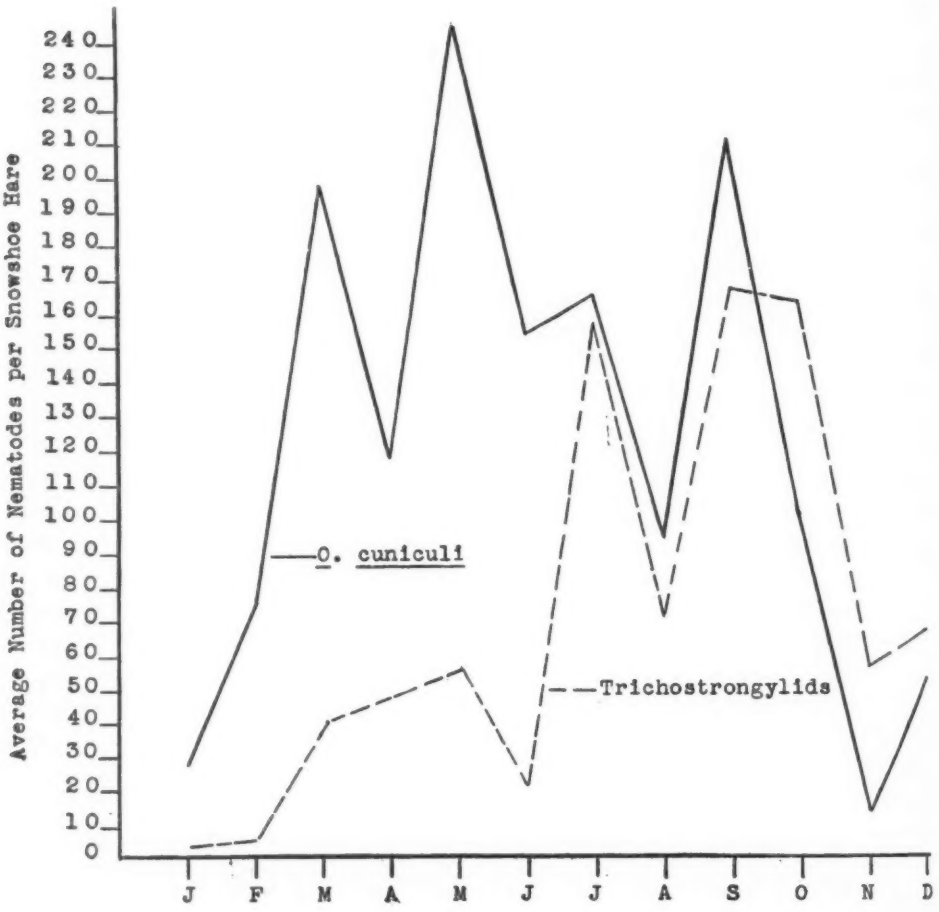
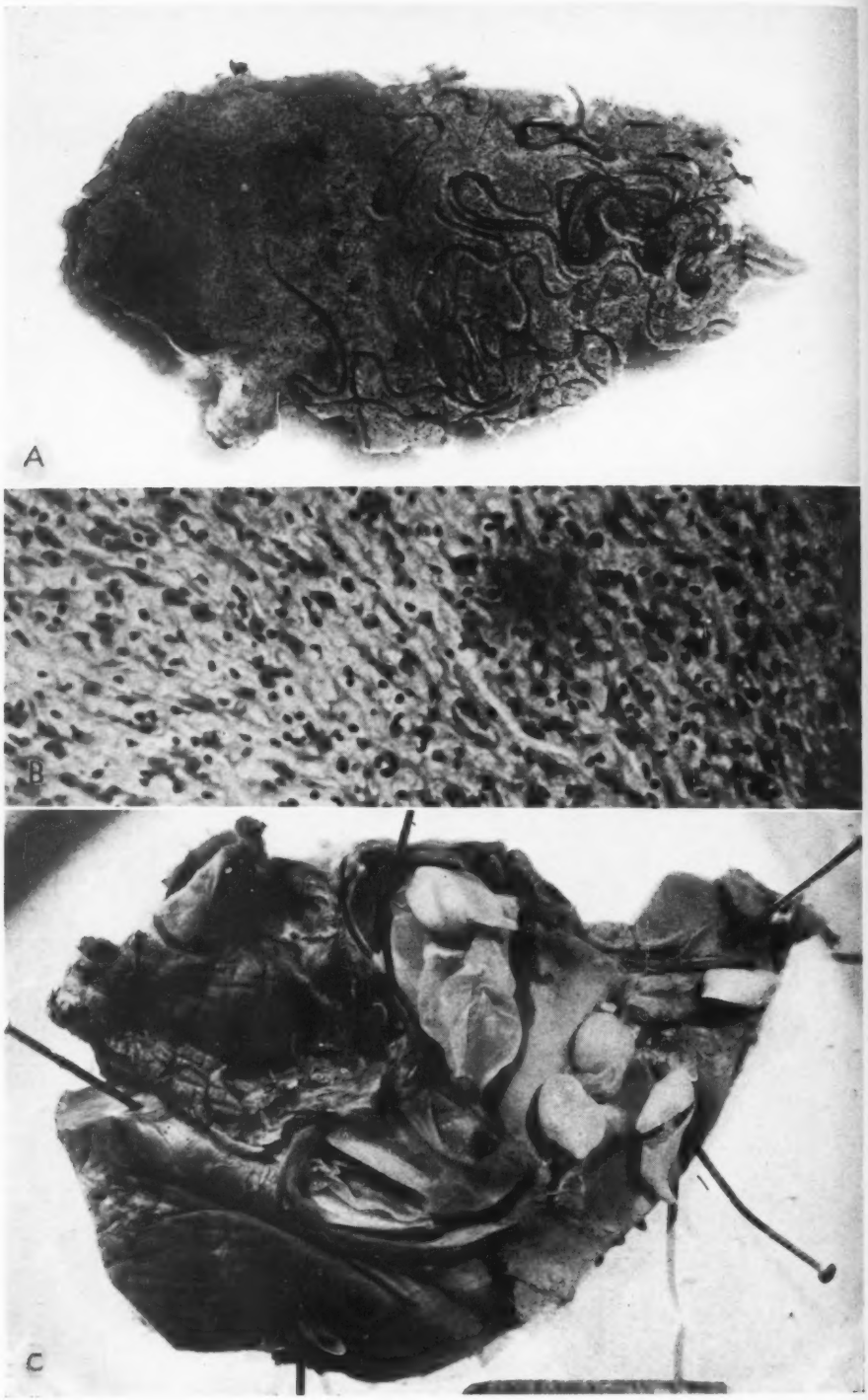


Fig. 3. Monthly variations in the average number of *Obeliscoides cuniculi* and trichostrongylids (*T. calcaratus*, *T. affinis*, and *N. triangularis*) found in snowshoe hares, 1931–40.



Snowshoe hare. *A*. Portion of stomach showing *Obeliscoides cuniculi* beneath the mucous membrane; ×2. *B*. Spindle cell sarcoma of the stomach; ×130. *C*. Cysts of *Taenia pisiformis* between the outer and inner walls of the stomach; ×2.

712 adults. A slowly acquired immunity may enable worm infestations to build up in hares until the host attains a certain age when the worms began to be eliminated. The total infection by 17 species of parasites was 91.1 per cent in the adults and 64.9 per cent among the immatures.

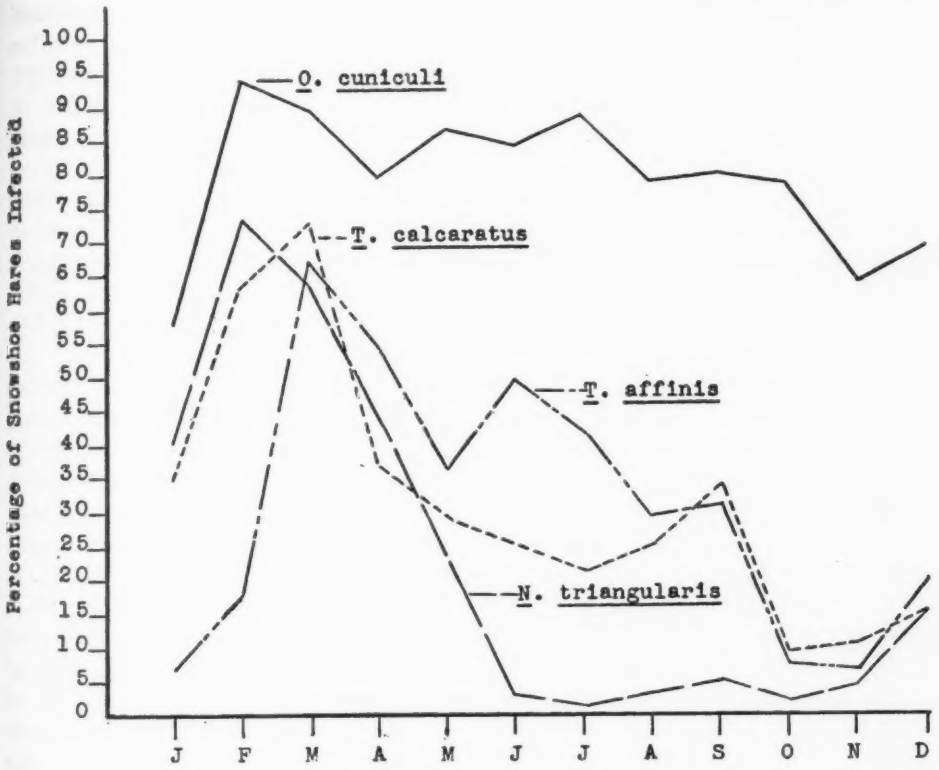


Fig. 4. Monthly variations in the percentage of snowshoe hares infected by four species of nematodes, 1931–40.

The lung worm (*Protostrongylus boughtoni*) is an important parasite that may cause mortality. Lungs of many hares were studied by Green, Larson, and Bell (1939) who stated that "during the period of decimation the incidence of lungworm (*Synthetocaulus leporis*) infestations among hares was greater than that of any other helminth parasite except stomach worms."

Boughton (1932) also found a high percentage of animals infected by this worm. Of 30 freshly killed hares, 25 were parasitized and often 50 to 60 worms were found in one lung lobe.

PATHOLOGY

Extensive parasitism of wild animals may not be accompanied by demonstrable pathological conditions but this affords no basis for believing that the parasites are harmless. There is little

information on the effects of parasitism in wild animals as compared with domestic forms, and to interpret host-parasite relations of wild species we must consider findings for domestic hosts harboring the same or similar parasites.

Heavy infections of stomach worms in domestic rabbits cause emaciation, diarrhea, anemia, ulcers, and death (Schwartz and Shook, 1935). Hemorrhages and erosion of the gastric glands have been noted by Alicata (1932).

MacLulich (1937) stated that stomach worms "were the cause of the only epidemic among hares studied in the field. . . . Of seven that died six had the stomach full of worms in yellowish, thick fluid. The hares did not eat for a day before dying in convulsions. The liver was dark red and congested. . . . It seems definite that the stomach worms caused these deaths."

In the present study additional information on the pathogenicity of the stomach worm was obtained. In 714 hares the average number of stomach worms was 170 and the maximum, 4,015. Frequently 300 to 600 worms were found per stomach, especially in hares collected during the die-off of 1935–38. Sometimes they were in the stomach contents, but usually lay next to the mucous membrane or partially under it (Pl. 7, A). Blood clots resulting from hemorrhages were frequent. In about 20 per cent of the stomachs that contained many worms and little food, the worms were concentrated in the cardiac and pyloric angles. The pyloric area was much thickened and the pylorus almost occluded so that normal movement of food must have been impossible. Green and Larson (1938) reported that of 174 hares examined in 1936, 34 had the pyloric valve thickened and contracted and their stomachs contained many worms.

The stomach of one hare (No. 3270) collected at Lake Alexander on June 9, 1939, contained 243 *O. cuniculi* and masses of sloughed stomach wall. On examining sections of this material (Pl. 7, B), Dr. E. J. Karolyi and Dr. R. Fenstermacher diagnosed the neoplasm as a spindle-cell sarcoma. Possibly the action of the worms initiated the tissue response which resulted in the sarcoma. Fibiger (1913), Bullock and Curtis (1920), and Cram (1934) have shown that sarcomas may be caused by helminths.

Stomach worm infections were more severe in older hares than in the young, indicating that infections tend to increase and resistance develops slowly. In 150 adults, heavily infected, both the intestines and stomachs held many worms apparently being eliminated. It is my belief that the stomach worm is important in producing pathological changes, in lowering the resistance of the host (possibly by the production of toxins), in some cases killing hares outright, and that it contributes to the fluctuations of hare populations.

Sarles (1932, 1934) showed that rabbits develop resistance to *Trichostrongylus calcaratus* when given increasing doses of infective larvae weekly. To produce an infection of 1,000 worms, which occasionally resulted in death without gross lesions, he found it necessary to give a rabbit 10,000 larvae.

Many hares examined by the writer, especially those collected from 1935–38, contained 300 to 1,000 worms, indicating that they had been exposed to

heavy infections of larvae. The health of hares probably is impaired by infections of *T. calcaratus*, and they may occasionally succumb to heavy infestations. Heavy infections of *T. affinis* probably produce symptoms similar to those of *T. calcaratus* although this has not been proved.

Boughton (1932) considered that a trichostrongylid, *Nematodirus triangularis*, could produce epizootics in hares. In the present study, this nematode was found most commonly in hares collected in 1936, especially those obtained in St. Louis, Pine, and Douglas counties, where many were found dead. Members of the genus *Nematodirus* are blood suckers, and cause anemia, loss of appetite, diarrhea, and death in various ruminants.

Little is known about the effect of species of *Passalurus* on their hosts. No definite pathology has been associated with heavy infections. The absorption of food or the secretions of toxins by the worms might injure the host. Evans (1940a) found rapid increase in the number of *P. ambiguus* up to the age at which rabbits (*Oryctolagus cuniculus*) weighed 3.5 pounds; then an age resistance set in and the infection was cast off. This suggests that toxins are produced by *P. ambiguus*.

The heaviest infection of *P. nonanulatus* was in a hare (No. 3351) found dead at Lake Alexander on April 23, 1938; its cecum contained an estimated 25,000 worms and the large intestine about 10,000 more. This hare probably succumbed to the massive infection. The average number in 197 infected animals was 1,192, but if No. 3351 is omitted, the average number was 566. Available data seem to indicate that heavy infections of *P. nonanulatus* may be definitely injurious although it is difficult to demonstrate any pathological changes.

One hare (No. 4081) shot at Lake Alexander on May 4, 1938 appeared to have developed an immunity and was in the process of casting off worms. Of *P. nonanulatus* it had 240 in the stomach, 579 in the small intestine, and 9,220 in the large intestine.

In many hares of which the writer examined the gastro-intestinal tracts, the lungs were studied by Green, Larson, and Bell (1939) who stated that of 174 dying of shock disease in 1936, 95 were infected with lung worms. In describing the pathology they wrote, "Gross pathological lesions, small areas of necrosis of the lungs and pleural adhesions, were produced by these parasites. . . . It is noteworthy that some of the hares that died of shock disease exhibited no evidence of lungworm infection." Boughton (1932) stated that "since this parasite [lungworm], even at present [1930–31], which is a time of minimum infestation, must have some effect upon the health of the rabbit population, it appears that in epidemic years, the numbers increase to such an extent that pneumonia sets in accompanied by other secondary diseases."

Heavy visceral infections by *T. pisiformis* may result in extensive liver damage, arrestment of growth, lack of fat, increase in amount of peritoneal fluid, and toxemia (Whitlock, 1939). The heaviest infection studied by the writer was in a hare (No. 5117) found dead at Lake Alexander on October 10, 1940. From its mesentaries, 70 cysts were removed. The gastro-intestinal tract was much enlarged. A hare shot

at Lake Alexander on August 10, 1936 harbored a most unusual infection of *T. pisiformis* cysts between the outer and inner walls of the stomach. These normally are thin, but in this hare had thickened as a reaction of the host tissue to the parasites (Pl. 7, C).

Miller and Kerr (1932), Solomon (1934), Evans (1940b), and Sima (1937) have shown that an immunity develops in rabbits subsequent to infection with *T. pisiformis*. Infections with this species probably do not have their greatest effect on hares at the time of peak populations but probably one or two years later when the peak fox and lynx populations have been attained. An increase in the number of these carnivores, which harbor the adult *T. pisiformis*, affords greater opportunity for the parasite to complete its life cycle, providing that hares have not declined to the point beyond which they are still easily accessible. In 1937 there were 167 hares per square mile on the Lake Alexander area. There is no information on the numbers of foxes and coyotes in that year, but 44.4 per cent of the hares examined were infected by *T. pisiformis*. This rate was 20 per cent greater than that for the next highest year (1939) and seems to indicate that a large population of primary hosts was available in 1937.

LESS IMPORTANT PARASITES

SPECIES

Thirteen other parasites (Table 1) were considered less important in producing mortality than the five already discussed; these were a trematode (*Euparyphium melis*), five tapeworms (*Cittotaenia pectinata americana, C. variabilis, Hymenolepis* sp., *Taenia* sp., and *Multiceps* sp.), three nematodes (*Nematodirus leporis, Dermatoxys veligera*, and *Trichuris leporis*), and four larval dipterans (*Fannia scalaris, Aphiochaeta xanthina, Sarcophaga* sp., and a schizophoran). Three of the worm parasites were more important than the others. *C. pectinata* was recovered from 62 of 720 or 8.6 per cent of the hares; *Multiceps* sp. from 47 of 773 or 6 per cent; and *T. leporis* from 161 of 720 or 22.3 per cent. All other parasites except the schizophoran occurred in less than one per cent of the animals.

The whipworm (*T. leporis*) reached a peak of abundance in 1935–36 when 36.7 and 33.5 per cent, respectively, of the hares were infected. Infections remained high through 1940 when 34 per cent were parasitized. From 1931 to 1934, when hare populations were increasing, the infected animals were significantly fewer (average, 12.6%) than from 1935 to 1940 when populations reached a peak and then declined (average, 28%).

Infections by *C. pectinata* and *Multiceps* sp. showed no marked peaks of abundance. Infections by the first did not vary more than about 5 per cent from year to year and of the second not more than 10 per cent. The largest numbers were infected by *T. leporis* and *Multiceps* sp. in late winter and early spring. Infections by *C. pectinata* reached their greatest intensity in summer and early autumn, when immature animals, more susceptible than adults, were more numerous.

There was no significant difference in infection of the two sexes by *T. leporis*, *Multiceps* sp. and *C. pectinata*, although the infection of adult and immature hares by the last was significantly dif-

TABLE 1.—WORM AND ARTHROPOD INFECTIONS OF SNOWSHOE HARES IN MINNESOTA, 1931–40

data summarized thus: 65 infected/103 examined / *63.1* percentage infected

Parasites	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1931–40
Obeliscoides cuniculi	65/103	50/89	27/45	77/96	106/109	141/152	13/18	20/27	30/34	29/41	558/714
	63.1	*56.2*	*60.8*	*80.2*	*97.2*	*92.8*	*72.2*	*74.0*	*88.2*	*70.7*	*78.1*
Trichostrongylus calcaratus	2/131	21/93	1/47	12/96	22/77	95/155	9/17	10/27	15/36	22/41	209/720
	1.5	*22.6*	*2.1*	*12.5*	*28.6*	*61.3*	*52.9*	*37.0*	*41.7*	*53.6*	*29.0*
Trichostrongylus affinis	8/131	32/93	4/47	22/96	31/77	70/155	10/17	15/27	12/36	25/41	229/720
	6.1	*34.4*	*8.5*	*22.9*	*40.2*	*45.2*	*58.8*	*55.5*	*33.3*	*61.0*	*31.8*
Nematodirus triangularis	2/131	22/93	0/47	16/96	5/77	67/155	2/17	6/27	10/36	12/41	142/720
	1.5	*23.6*	*0.0*	*16.7*	*6.5*	*43.2*	*11.8*	*22.2*	*27.8*	*29.3*	*19.7*
Nematodirus leporis	0/131	0/93	0/47	1/96	0/77	0/155	0/17	0/27	0/36	0/41	1/720
	0.0	*0.0*	*0.0*	*1.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.1*
Passalurus nonanulatus	24/131	37/93	6/47	16/96	37/77	55/155	4/17	7/27	8/36	3/41	197/720
	18.3	*39.8*	*12.8*	*16.7*	*48.0*	*35.5*	*23.5*	*25.9*	*22.2*	*7.3*	*27.4*
Dermatoxys veligera	0/131	0/93	1/47	1/96	0/77	1/155	0/17	0/27	0/36	0/41	3/720
	0.0	*0.0*	*2.1*	*1.0*	*0.0*	*0.7*	*0.0*	*0.0*	*0.0*	*0.0*	*0.4*
Trichuris leporis	18/131	11/93	4/47	16/96	28/77	52/155	3/17	5/27	10/36	14/41	161/720
	13.7	*11.8*	*8.5*	*16.7*	*36.7*	*33.5*	*17.6*	*18.5*	*27.8*	*34.1*	*22.4*
Taenia pisiformis	31/149	15/94	11/47	9/96	19/109	31/155	8/18	3/27	9/36	8/41	144/772
	20.8	*15.9*	*23.4*	*9.4*	*17.4*	*20.0*	*44.4*	*11.1*	*25.0*	*19.5*	*18.6*
Taenia sp.	1/131	0/93	1/47	0/96	0/77	0/155	0/17	0/27	0/36	0/41	2/720
	0.8	*0.0*	*2.1*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.3*
Multiceps sp.	1/149	5/94	9/48	7/96	7/109	7/155	3/18	2/27	3/36	3/41	47/773
	0.7	*5.3*	*18.7*	*7.3*	*6.4*	*4.5*	*16.7*	*7.4*	*8.3*	*7.3*	*6.1*
Cittotaenia pectinata	14/131	6/93	8/47	3/96	13/77	5/155	1/17	3/27	4/36	5/41	62/720
	10.7	*6.4*	*17.0*	*3.1*	*16.9*	*3.2*	*5.9*	*11.1*	*11.1*	*12.2*	*8.6*
Cittotaenia variabilis	0/131	0/93	0/47	0/96	0/77	0/155	0/17	0/27	0/36	1/41	1/720
	0.0	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*2.4*	*0.1*
Aphiochaeta xanthina	0/131	2/93	0/47	0/96	0/77	0/155	0/17	0/27	0/36	0/41	2/720
	0.0	*2.1*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.3*
Fannia scalaris	0/131	0/93	0/47	0/96	0/77	1/155	0/17	0/27	0/36	0/41	1/720
	0.0	*0.0*	*0.0*	*0.0*	*0.0*	*0.6*	*0.0*	*0.0*	*0.0*	*0.0*	*0.1*
Sarcophaga sp.	0/131	0/93	0/47	1/96	0/77	0/155	0/17	0/27	0/36	0/41	1/720
	0.0	*0.0*	*0.0*	*1.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.1*
Schizophora	0/131	0/93	0/47	0/96	0/77	9/155	0/17	0/27	0/36	0/41	9/720
	0.0	*0.0*	*0.0*	*0.0*	*0.0*	*5.8*	*0.0*	*0.0*	*0.0*	*0.0*	*1.2*
Total infections/total examined	113/149	86/94	39/48	80/96	109/109	151/151	17/18	26/27	32/36	37/41	690/769
percentage infected	*75.9*	*91.5*	*81.2*	*83.3*	*100.0*	*100.0*	*94.4*	*96.3*	*88.9*	*90.2*	*89.7*

ferent; of 57 immatures, 19 (33%) infected and of 672 adults, 43 (6.4%).

Only one hare, collected at Lake Alexander on July 9, 1936, was infected by the trematode (*Euparyphium melis*), normally a parasite of mustelids (Erickson, 1940a). Two hares, collected in June and August 1937 at Lake Alexander, were infected by *C. variabilis*. These are the first records for the species in the snowshoe hare. A fragment of a tapeworm (*Hymenolepis* sp.) was recovered from one hare killed at Lake Alexander in July, 1936, the animal had been in captivity for about a month.

Larvae of a tapeworm (*Taenia* sp.) were recovered from the intestines of eight hares at Lake Alexander; six in captivity and two killed in the wild. The maximum number of larvae in any individual was nine. This species is probably an accidental parasite of the hare, entering with food and passing through unchanged. The larval cysts

averaged 5 mm. in length and were elongate, not rounded like the mature cysts of *T. pisiformis*. The rostellum had a double circle of hooks, with 19 or 20 in each; the large hooks were 182–190μ long and the small ones 129–133μ. The hooks were shorter than those of *T. pisiformis* and of different shape, and did not correspond closely to those of any described species as to number or measurements.

One hare infected by 33 *Nematodirus leporis* was collected at Lake Alexander, on June 9, 1934 (Erickson, 1940b). Three (0.41%) of 720 hares were infected by the nematode *Dermatoxys veliger*, the maximum number of worms being 42 and the average 6.

The four species of larval Diptera are considered spurious parasites of the snowshoe hare, and all appear to be first records for this host. One hare collected in Pine County, March 12, 1936, contained *Fannia scalaris*. *Aphiochaeta xanthina* was recovered from two collected at Lake Alexander on November 11, 1932. *Sarcophaga* sp. was recovered from one collected in the Brule State Forest, Douglas County, Wisconsin, May 22, 1934. Nine hares (1.25%) contained larvae which belong to the dipterous subsection Schizophora. The hosts were collected in 1936, eight near the St. Croix River, Pine County, Minnesota, March 3 to 14, and one in St. Louis County, February 3.

PATHOLOGY

In the snowshoe hare the ileum has only a small lumen which one large or several small tapeworms (*C. pectinata*) could occlude. A hare (No. 4430) shot at Lake Alexander on July 19, 1939 contained five large *Cittotaenia;* its intestine was completely occluded and had telescoped for a distance of six inches so that passage of food must have been impossible.

Infections by *C. pectinata* in immature hares seem to induce a high degree of immunity, whether absolute or not is unknown. The 6 per cent of infections in adult hares indicates that either reinfection is possible or these animals had not been infected when young. *C. pectinata* occasionally may affect the health of its host or even produce death by mechanical obstruction of the intestine; in general, it is probably benign, with little influence on fluctuations in hare populations.

A few records of large cysts of *Multiceps* sp. were obtained. Large cysts can interfere with locomotion and the function of the organs and may cause death.

One nematode (*Dermatoxys veliger*) was so infrequent that it could have no possible influence on host abundance. Heavy infections of fourth-stage larvae, however, may be pathogenic (Wetzel, 1931).

There is no information as to pathology produced by whipworms (*Trichuris leporis*). A hare (No. 5126) which died in captivity at Lake Alexander in 1940 contained the heaviest infection: there were 357 in the cecum, the heads of all being imbedded in the mucosa. In another there were 166 worms attached securely to the wall of the cecum. Usually, however, infections were light, and the worms did not produce pathological conditions that could have influenced the numbers of hares.

CONCURRENT INFECTIONS, 1931–40

A heavy infection by helminths of one species sometimes is sufficient to

cause the death of a hare. A lighter infection by two species may accomplish the same end. When there are three or more kinds and in large numbers a complicated condition results, as for example in the stomach (*Obeliscoides cuniculi*), small intestine (*Trichostrongylus calcaratus*), caecum (*T. affinis*), liver and mesentaries (*Taenia pisiformis*), skeletal muscles (*Multiceps* sp.), and lungs (*Protostrongylus boughtoni*). Each requires food; some suck blood; some subsist on the contents of the stomach and intestines; and some of them are imbedded in the muscles or mesentaries awaiting ingestion by the primary host. In addition, some parasites produce toxins that further injure the host. Heavy multiple infections as occurred in many Minnesota hares from 1935 to 1939, undoubtedly reduce resistance in the host animals so that they will succumb more readily to adverse conditions, which they otherwise would survive.

Of 774 hares, seven (1%) contained seven species of parasites; 28 (4%) had six; 60 (8%) had five; 98 (13%) had four; 116 (15%) had three; 176 (23%) had two; 209 (27%) contained one species; and 82 (11%) held no parasites. The complete data by years on concurrent infections are given in Table 2.

It is significant that the largest percentages of hares with three or more concurrent parasitic infections were found from 1936 to 1939 when the die-off was most severe. A peak of concurrent infections was reached in 1936–37 for hares harboring up to four species; that with three species occurred in 1938–39. Hares with two, one, or no species were least abundant from 1936 to 1940, and therefore more abundant from 1931 to 1934 when hare populations were increasing. (Compare Figs. 5 and 1.)

TABLE 2.—CONCURRENT INFECTIONS OF SNOWSHOE HARES IN MINNESOTA, 1931–40
data summarized thus: 28 infected/*19* per cent of all examined during year.

Year	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1931–40
Hares examined	(149)	(94)	(48)	(96)	(109)	(155)	(19)	(27)	(36)	(41)	(774)
Species of parasites per hare											
7	0/ *0*	0/ *0*	0/ *0*	0/ *0*	0/ *0*	6/ *4*	0/ *0*	0/ *0*	0/ *0*	1/ *2*	7/ *1*
6	1/ *1*	1/ *1*	1/ *2*	4/ *4*	2/ *2*	14/ *9*	0/ *0*	2/ *7*	2/ *6*	1/ *2*	28/ *4*
5	0/ *0*	7/ *8*	1/ *2*	5/ *5*	6/ *6*	25/*16*	5/*26*	2/ *7*	3/ *8*	6/*15*	60/ *8*
4	3/ *2*	13/*14*	1/ *2*	7/ *7*	16/*15*	37/*24*	4/*21*	2/ *7*	6/*17*	9/*22*	98/*13*
3	7/ *5*	15/*16*	6/*13*	11/*11*	20/*18*	25/*16*	3/*16*	10/*37*	9/*25*	10/*24*	116/*15*
2	28/*19*	17/*18*	16/*33*	22/*23*	42/*39*	31/*20*	2/*11*	4/*15*	8/*22*	6/*15*	176/*23*
1	75/*50*	33/*35*	15/*31*	31/*32*	24/*22*	13/ *8*	4/*21*	6/*22*	4/*11*	4/*10*	209/*27*
0	32/*23*	8/ *9*	9/*19*	16/*17*	0/ *0*	4/ *3*	1/ *5*	1/ *4*	4/*11*	4/*10*	82/*11*

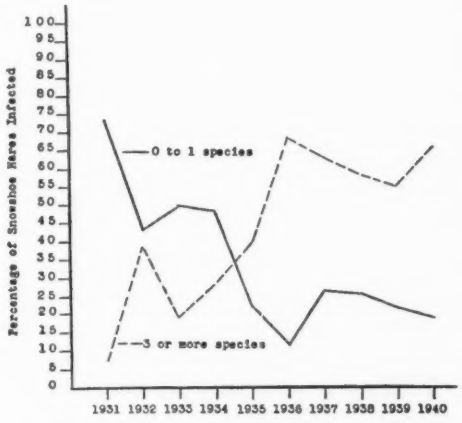


Fig. 5. Yearly variations in the percentage of hares infected by one or no species of parasite, and by three or more species.

INFECTIONS IN FOUR AREAS

The numbers of hares present in a region may differ greatly in local areas separated by a few hundred miles or less. Parasites likewise may fluctuate in numbers in the hosts from area to area. The fluctuation of parasites appears to be related largely to differences in meteoro-topographical conditions (Boughton 1932, 1937), but also is related closely to the degree of resistance to disease and parasites that the individual animals of a community have attained.

In 1936 hares were obtained from four areas in Minnesota: east-central, 57; north-eastern, 17; central, 58; and north-central, 19. In each, helminth infestations both as to numbers of species and numbers of worms per hare were high, indicating a peak of parasitic infection over the entire hare range in Minnesota about 1936. Infections by the stomach worm ranged from 90 to 100 per cent in all four areas. The percentage of infections by trichostrongylids (*T. calcaratus* and *T. affinis*), were high in all four areas and highest in east-central Minnesota. Infection by a trichostrongylid (*Nematodirus triangularis*) was highest in the north-eastern area, where 94 per cent of the hares were parasitized. The infections by all but two species (*Trichchostrongylus affinis* and *Taenia pisiformis*) were lowest in north-central Minnesota.

INFECTIONS IN WILD AND CAPTIVE HARES

Parasitic infections were compared in two groups of hares, one of 179 animals kept in 1.7 acre enclosures for an average of three months, and the other of 277 animals collected in the wild. All were collected from 1936 to 1940; no "enclosure hares" were available before those years. Often 40 were held in the enclosures at one time, whereas the population then in the wild was never more than 1.5 per acre.

The percentage infected by *O. cuniculi* was about 26 per cent greater among "wild hares" than in infected "enclosure hares," and the percentage infected by *Nematodirus leporis* was about 20 per cent greater. Infections by *T. calcaratus* and *T. affinis* were about 50 per cent in both groups.

The lesser degree of parasitism among the "enclosure hares" than those freshly caught may have been due to the presence of more immature individuals in the enclosure group and that immature animals tended to have fewer species and numbers of parasites than adults.

PARASITES AND SHOCK DISEASE

One object of this study was to watch for any possible correlation between helminth parasitism and shock disease. Gastro-intestinal tracts of 31 among 174 hares that died of shock disease in Pine County during 1936 were available. The incidence of parasitism, by species and individual worms, was high in them but not markedly different from infections in other animals collected in the same or other areas during that year. No definite conclusions seem warranted because almost the entire hare population of Pine and Douglas counties in 1936 was afflicted with shock disease to some degree (Green, Larson, and Mather, 1938). Shock disease is correlated with die-off of hares; heavy infections of helminths are correlated with die-off; and possibly there is a relation between heavy infections of helminths and shock disease.

DISCUSSION

The snowshoe hare is a primary cyclic species. The lynx and fox which prey upon it are secondary cyclics, but never seem to become abundant enough to bring about a noticeable decrease in the hares; they kill directly and the death of one hare does not greatly affect the health or activity of remaining hares. When the hares die off, lynxes and foxes subsequently do likewise, but their decrease lags a year or two. In similar manner, when the hares increase, the lynxes and foxes also multiply, but their increase lags because of their lower biotic potential.

The helminths of the hares also may be considered as secondary cyclic; they exhibited regular fluctuations in numbers in hare populations from 1931–40. The stomach worm and the trichostrongylids, for example, were not abundant from 1931 to 1933; but as hares increased in 1934–35, the percentage of infected animals became greater and the worm burden heavier. Hare populations declined extensively in 1935, but worm-infested hares were still abundant. By 1939–40, nematode populations, while still high, had dropped, indicating a lag behind that in the hares. Being parasites they seldom kill directly; rather they affect the well-being of their hosts indirectly and this is probably cumulative.

Several characteristics of the snowshoe hare make it unusually susceptible to invasion by helminths and protozoa, coprophagy being one of these. Fecal pellets were found in the stomachs of a number of hares. Many other stomachs probably contained feces, but the pellets had lost recognizable form and merged with other materials. Fecal pellets may contain many helminth ova and coccidial oocysts, which soon develop to infective stages, and habitual coprophagy would quickly spread them from hare to hare. Several authors (Madsen, 1939; Southern, 1940; Eden, 1940) have discussed the coprophagous habit of rabbits.

The small daily and yearly cruising radius of the hare is another characteristic which makes it vulnerable to parasites. This is especially true in late winter and early spring when it is confined to narrow runways by deep snow.

SUMMARY

The gastro-intestinal tracts of 953 showshoe hares, collected in Minnesota from September 1931 through December 30, 1940, were examined for helminth parasites. The animals were taken during all seasons and represented many of both sexes and all age classes. Particular attention was given to the effect of helminth parasitism on the fluctuation of hare populations.

The following helminths were considered significant in causing mortality: stomach worm (*Obeliscoides cuniculi*), trichostrongylids (*Trichostrongylus calcaratus*, *T. affinis*, and *Nematodirus triangularis*), pin worm (*Passalurus nonanulatus*), and larvae of a tapeworm (*Taenia pisiformis*).

Parasites were not abundant from 1931 to 1933, when hare populations were building up; but gradually they increased and by 1935–36 a peak of parasitism by six species of nematodes and two species of cestodes was reached, when the hares began to die off.

There was no significant difference in the percentage of infection by sexes, but the percentage of infections of adults

and immatures for some parasites differed markedly.

The largest percentage of hares was infected with parasites in late winter and early spring. The highest average numbers of stomach worms and trichostrongylids were recorded in March, May, July, and September.

The highest percentages of concurrent infections of parasites were found from 1936 to 1940 when hares were dying in the largest numbers.

In 1936, 151 hares were obtained from four areas. Helminth infections by species and individuals were high, indicating a peak of parasitism then over the entire snowshoe hare range in Minnesota.

In 179 hares held in 1.7 acre enclosures for an average of three months infections by two nematodes (*O. cuniculi* and *Nematodirus leporis*) were less than among 277 hares collected in the wild.

Among 31 hares dead of shock disease in 1936 in Pine County, Minnesota, the incidence of parasitism was high, but not markedly different from that in hares collected over the entire state in the same year.

One hare had an unusual infection of *T. pisiformis* cysts between the outer and inner walls of the stomach; these layers were much thickened, a possible reaction of the host tissues to the parasites.

Stomach worms usually were found next to or partly beneath the mucous membrane. Clotted blood, resulting from hemorrhages produced by the worms, was frequent; in about 20 per cent of stomachs the pyloric valve was much thickened so that normal movement of food must have been impossible.

The stomach of one hare contained 243 stomach worms and masses of sloughed stomach wall; this material proved to be a spindle-cell sarcoma, possibly initiated by the worms.

The heaviest infection by *P. nonanulatus*, of an estimated 35,000 worms, probably caused the death of one hare.

Heavy infections of *T. calcaratus* and *T. affinis* seemed not to produce pathological conditions. These two hookworms and also *O. cuniculi* and *N. triangularis* probably produce toxins injurious to the host.

Stomach worms, trichostrongylids, pin worms, and tapeworm larvae (*T. pisiformis*) apparently were important in reducing the resistance of hares to other decimating factors and in killing some animals outright by sucking blood (stomach worm and trichostrongylids), by utilizing food, by producing toxins (*T. calcaratus* and probably *T. affinis*, *O. cuniculi*, and *Protostrongylus boughtoni*), and by causing erosion of the gastric glands, inflammation and thickening of the pyloric valve, spindle-cell sarcoma (stomach worms), liver damage (*T. pisiformis*), and lung damage (*P. boughtoni*), thus directly or indirectly influencing the decline of hare populations in Minnesota from 1935 to 1939.

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DOUGLAS GROUND SQUIRREL AS A PREDATOR ON NESTS OF UPLAND GAME BIRDS IN OREGON[1]

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It is commonly recognized that various species of ground squirrels are partly predatory in nature, but relatively little intensive study has been made of the problem. In California, the Beechey ground squirrel has been studied (Emlen and Glading, 1938; Horn, 1938a, b, 1939) in relation to the valley quail (*Lophortyx californica*) but no data are available as to predation on pheasant nests by this or other species. The in-

[1] This study was made under direction of the Department of Fish and Game Management at Oregon State College, and financed by the Oregon Cooperative Wildlife Research Unit (U. S. Fish and Wildlife Service, Oregon State College, Oregon State Game Commission, and American Wildlife Institute, cooperating).

vestigation here reported was made during the nesting season of 1940 for upland game birds in the Willamette Valley, Oregon. Effort was made to determine whether the Douglas ground squirrel (*Citellus beecheyi douglasii*) is a factor in nesting losses of the ring-necked pheasant (*Phasianus colchicus torquatus*) and the bobwhite quail (*Colinus virginianus*), and if so, to estimate its importance.

The field work was done on an experimental area of some 5,000 acres of farm land, closed to hunting for the previous four years, where certain predatory species of birds and mammals have been controlled during the same period. Only the one species of ground squirrel is present, and known locally as the "gray digger." Pheasants and quail occur throughout the area.

STUDY OF DUMMY NESTS

One hundred dummy nests (86 pheasant, 14 bobwhite) were made to imitate wild nests as closely as possible, considering the varied environments in which they were placed, and a small steel trap set at each. The surroundings were left as natural as possible, and proper precautions were taken whenever the nests were visited. A detailed record was kept for each, including the following items which might influence predation: time of season; distance from nest to nearest squirrel burrow; value of the location as a game bird habitat; number of eggs in the clutch; and type and degree of cover at the nest. These nests and traps were operated from April 25 until August 25, except for a ten-day interval in early June. This period corresponds closely with the local nesting season. Individual sets remained in place from one to 36 days (average 12), a total of 1,204 trap-days.

The results were recorded as to date, species and sex of all animals caught, direct evidence such as hair or claws in sprung traps (or lack of such evidence), and the condition of the eggs—whether eaten, stolen, or untouched. A stomach analysis was made of most of the animals caught, especially if the eggs had been molested.

Eighty of the 100 nests were disturbed at some time; 59 of the traps caught some predatory species of bird or mammal, including the ground squirrel; 8 held direct evidence such as claws or hairs; 10 were sprung, but contained no incriminating evidence; and at 3 other nests only the eggs were disturbed. Many of the sets made repeated catches. The kinds and numbers of animals caught were as follows:

Species	*Sets raided*	*Individuals caught*
Douglas ground squirrel	43	70
Striped skunk (*Mephitis occidentalis*)	21	22
Long-tailed jay (*Aphelocoma californica*)	3	4
House cat (*Felis catus*)	2	2
Brown rat (*Rattus norvegicus*)	1	2
Coast jay (*Cyanocitta stelleri*)	1	1
Gray fox (*Urocyon cinereoargenteus*)	1	1

Direct evidence, in addition to the catches listed, included, for the squirrel: remains of toes or claws in trap, 14; and hair, 6. A total of 90 individuals was definitely identified. For the skunk, hair was identified at one trap and eggs, eaten in characteristic skunk manner, at another nest, making a total of 24 skunks identified. Seventy-one traps were sprung without sufficient evidence remaining to determine the cause. These

are disregarded in the following calculations.

Of the 100 sets, eggs were molested in some manner at 58, stolen from 42, and eaten at 34. Counting repeated raids, 152 eggs were missing on 76 inspection visits, and in all 126 eggs were eaten on 46 occasions. The condition of the eggs, when the 124 predators definitely identified were caught, may be summarized as follows:

Species	*Recovered in stomach*	*Eaten; not recovered*	*Some stolen*	*Intact or broken*
Douglas ground squirrel	3	4	27	56
Striped skunk	13	3	4	4
Long-tailed jay		2	1	1
Coast jay		1		
House cat		1		1
Gray fox			1	
Brown rat		1(?)		1

Although the average nest was exposed for less than half of the normal period of incubation for the bird species concerned, 80 of the 100 dummy nests were visited by some species of predatory animal; 52 per cent were raided more than once and some as often as eight or ten times. Such nests were restocked with eggs between visits, and made to look as natural as possible. In one instance (Set 35) two squirrels were taken from the same nest-set during the day following its construction. A young skunk destroyed that nest four days later. On one of the few occasions when two traps were placed at one nest, two digger squirrels were caught at the same time. A skunk was caught there the next day.

The largest number of predators caught at dummy nests on any one day was six. With twelve traps in operation on May 20, the catch consisted of two skunks, two jays, and two squirrels. On June 25, four of the ground squirrels were taken at eleven nests, and on July 26 three skunks and two squirrels were trapped at five of the 17 sets then in operation. On August 14 two skunks and three squirrels were taken in a total of 26 traps. On August 25 when 17 traps were set, five squirrels the most taken in one day, and one skunk were caught.

Although nearly three of every four individuals caught were Douglas ground squirrels, egg shells were actually recovered from only three stomachs of this species. There were, however, the following occasions when these squirrels almost certainly ate eggs at nests. One nest of six pheasant eggs in light grass cover under an oak tree and only six feet from the nearest burrow, was raided on five different dates. Some or all of the eggs had been stolen on four of these occasions and one squirrel was caught. On May 20, a second squirrel was trapped and only the broken shells of two eggs remained; the stomach was empty. At another pheasant nest, situated in heavy grass along a fence row, a fourth young squirrel was taken. One egg remained intact and the other was represented by an empty shell. Only green vegetation was identified in the squirrel's stomach. At another nest along a fence row and 30 feet from the nearest known burrow, a young squirrel was trapped on July 22; two of the six pheasant eggs were broken into as if eaten, but no shell was detected in the squirrel's stomach. Another squirrel was caught on August 14 at a pheasant nest in a harvested grain field; the nest was at least 50 feet from the nearest den. One partly eaten egg remained at the nest, the shell of one egg was found

about ten feet away, and the two others had disappeared. The animal's stomach was empty. In each of these cases the condition of the shells indicated that the eggs had been eaten rather than merely broken or crushed. Eggs belonging in this latter category were also recorded at times. It should be recognized that a stomach analysis reveals only the last meal of an animal. For adequate material to make accurate identifications, the analysis must be undertaken shortly after the meal is eaten. This was not always possible, because the traps were visited only once or twice a day.

Many of the squirrels must have been caught before reaching the eggs, and once trapped they immediately concentrated on attempting to escape. According to the record, this probably happened to 54 (60%) of those caught. Another reason for finding so few stomachs from trapped animals that contained egg shells is the habit of the Douglas ground squirrel of removing the eggs singly from the nest, rather than eating them on the spot. This may account for a score of cases where an animal was trapped at a nest from which some eggs were missing without a trace remaining, while other eggs were still intact. These squirrels apparently were caught on their second, third, or subsequent trips. The following are a few examples illustrating this habit.

During August, a squirrel was caught at a pheasant nest containing four eggs; two remained intact, one was missing, and the broken shell of the fourth was found some feet away. A more convincing incident occurred when a dummy nest of five bobwhite eggs, located about twenty feet from a digger squirrel's burrow, lost four eggs. They were recorded as having "disappeared," and the remains of the nest were left as found. On the following day, the broken shells of four bobwhite eggs were found mixed with some freshly removed soil at the entrance of the nearby squirrel burrow. On several other occasions a squirrel was trapped at a nest and a missing egg was found, broken, some distance away. No squirrel ever was actually observed carrying a pheasant egg, but several were seen while eating them. On one occasion a squirrel was seen to approach and carry off a bobwhite egg which had been placed near a den for observation purposes. Eggs were stolen from nests in 49 instances without the predators leaving any clues. How many of these records should be attributed to the Douglas ground squirrel, can only be conjectured. In some cases the egg appeared to have been dropped but not eaten. Examination of several pheasant eggs carried or eaten by these squirrels revealed that the animal pierces the shell on opposite sides with its long incisor teeth.

No significant difference was found in the results as to whether pheasant or bobwhite eggs were used for the dummy nests. Data on several items which varied from nest to nest were recorded carefully in the hope that one or more might prove to be of importance; these were: time of season (April to August), distance of nest from nearest squirrel burrow, rating of the site as a game bird habitat, number of eggs in the set, and the type and density of cover. Two of them proved to be significant.

The fact that this field study was carried on through only one nesting season,

and on a limited area, should be considered when evaluating the results. It is believed, however, that the results obtained warrant certain conclusions.

Nests in proximity to burrows are particularly susceptible to destruction, as might be expected from an animal like the Douglas ground squirrel which has a short cruising radius from a definite home site. Of those within 10 feet of a vegetative growth-form. Cultivation is self-explanatory. The degree of cover as expressed by light, moderate, and heavy is a general estimate based on personal judgement. The data of the table show a decidedly higher percentage of destruction for nests in grass cover than of those in weeds or brush. Cultivated land is somewhat intermediate, but approaches the grass habi-

TABLE 1.—RELATIONSHIP OF PREDATION BY GROUND SQUIRRELS ON GAME BIRD NESTS TO TYPE AND DENSITY OF COVER

Cover	No. of nests	Trap-days	Percentage of sets catching squirrels	Squirrels caught	Trap efficiency[a]	Percentage of sets molested
KIND						
Grass	39	488	*67*	47	9.6	*89*
Herbs	16	214	*37*	7	3.3	*63*
Brush	18	179	*39*	8	4.5	*67*
Cultivated	26	308	*46*	28	9.1	*77*
DENSITY						
Light	7	63	*43*	4	6.4	*100*
Moderate	41	463	*49*	41	8.9	*78*
Heavy	52	678	*54*	45	6.6	*79*

[a] Individuals caught ÷ trap days × 100.

den 75 per cent were raided as compared to an average of about 45 per cent for nests at greater distances. All such dens were not definitely known to have been in use at the time. On the basis of the number of times raided per number of days exposed, nests within 10 feet of a squirrel burrow may be judged twice as vulnerable as any others. Nearly one-third of all the squirrels taken were caught at such nests. Many of the 40 squirrels caught at undetermined distances from dens probably had travelled less than 100 feet, but it is common knowledge that these rodents may travel several times as far when in search of food.

In Table 1, the terms grass, herbs, and brush indicate the predominant tat as to danger from squirrel predation. Sets on cultivated land were practically confined to fields of grain and legumes in various stages of growth or following the harvest. The sets were usually less than 100 feet out in a field. That the comparatively low degree of destruction by squirrels in herb and brush cover did not result from other predatory species discovering the sets first, is shown by comparison of the figures for the total percentage of sets molested with those for squirrels alone. Nests in moderate cover appear to have been found more quickly than those in heavier cover, but eventually about the same percentage of nests in each group were raided. Only seven were placed in light cover, but all were destroyed.

There is an indication that nest damage by predation is more severe in cover along fence rows. Of the 80 nests molested by all predators, 47 (89%) of those along fence rows and 33 (70%) of all others were destroyed; for ground squirrel predation the figures were 30 (57%) and 21 (45%), respectively.

STOMACH ANALYSES

A routine field analysis of the digestive tract was made of each individual taken in traps at the dummy nests. In addition, ground squirrels were shot or trapped as opportunity afforded during the seven months of their active season. In all, 234 squirrel stomachs were examined, of which 30 were empty. Pheasant eggs, the primary object of the analyses, were identified positively in the stomachs of three squirrels caught at dummy nests. No evidence of egg eating was discovered in any animal not trapped at a nest. This does not necessarily imply that such predation does not take place, because it is necessary to examine the stomach shortly after the nest has been raided. The usual procedure of a ground squirrel is to remove the eggs, one at a time, and carry them some distance away before eating or storing them in their burrows. The stomach examinations indicated that the local squirrels were feeding principally upon green vegetation, fruits and seeds, of which about one-fourth came from cultivated crops. Animal matter amounted to about 1.5 per cent by volume and occurred in 13.7 per cent of the 204 individuals. In addition to the eggs, this included such items as insects and feathers, together with flesh and hair believed to have been of their own species.

OBSERVATIONS ON CAPTIVE SQUIRRELS

As a further check upon the egg eating propensities of the Douglas ground squirrel and to substantiate the stomach analysis data, eight individuals were taken in box traps and kept under observation in separate wire cages. They were caught at various times during July and August, and held for periods ranging of four to 38 days each. Both pheasant and bobwhite eggs were available to the squirrels throughout most of these observations. All items eaten or refused by them were recorded during a total of 136 animal-days. In general, the results confirmed those of the stomach analyses, and also afforded some interesting data on egg eating.

Pheasant and bobwhite eggs placed in the cages received quite unlike treatment by different squirrels. One, having both kinds of eggs available, ate the first bobwhite egg three days after it was placed in the cage and another egg remained twelve days before being eaten. During all of this time, a pheasant egg was unmolested. On August 26, after 24 days, the observer made a hole through the shell by reaching into the cage with a wire, and making an opening about $\frac{1}{8}$ inch in diameter; a single drop of the egg contents appeared on the shell. As soon as things quieted down the squirrel began to move about, apparently smelled the egg, and looked it over. Immediately she began to break off bits of the shell at the spot punctured, and to eat the egg. She was frightened off accidentally several times, but always returned within a few minutes and continued to eat into the egg. This individual had been well fed at all times and had eaten wheat, apple, cracker, and raisins already the same

morning, some just previous to finding the egg, and other food was still available in the cage. An hour or two later the egg had been eaten almost entirely, and the hole had been enlarged to about the size of a dime. Later, when the two kinds of eggs again were offered, the bobwhite egg was eaten within a day or two, but the pheasant egg, even with a hole through its shell, was not. Another squirrel, captive only four days, refused all eggs. Two young squirrels kept in one cage ate half of both kinds of eggs given them. One pheasant egg had been undisturbed for over two weeks when it was pierced with a wire as described previously. Upon inspection a few hours later, the egg had been eaten clean, and there was a large hole in it. Of the two captive adults, one individual ate a perfect egg and refused another, the second ignored the intact egg in his cage. When a hole was made through the shells, one squirrel ate his, but the other did not. One squirrel ate a bobwhite egg and another refused such an egg.

Such unpredictable behavior is difficult to analyze. During the experiments an effort was made to eliminate situations which might influence the results. At no time were any of the animals starved into eating the eggs. Normally they were fed at least three times a day. Fresh apples, a favorite food, were always available. The cages were small enough so that there was no possibility of an egg being overlooked. So far as known, all of the eggs were in similar condition, being freshly culled eggs obtained from the Corvallis State Game Farm.

The eggs eaten by the captives had more shell gnawed away than those eaten under more natural conditions. Whether there is any particular significance to this fact, such as an attempt to correct a dietary deficiency, is unknown. This seems unlikely since all shells were eaten to about the same extent. Furthermore, one individual ate an egg on the day following its capture, while some others did not do so for six and eight days. In the field, at a spot where some pheasant eggs had been eaten previously, a squirrel was twice observed to pick up a large piece of shell and gnaw on it. The two instances in which pheasant eggs were unmolested for two and three weeks but eaten shortly after the shell was penetrated may indicate that the animal had been unable to open the egg, or that it responded to the senses of taste or smell. The young squirrels used were almost the size of adults; it may be significant that neither of them ate any pheasant egg so long as the shell was intact, but one adult did take such an egg. In two of four cases, however, when the shells were pierced, young squirrels ate the eggs almost immediately. Contrary evidence may be taken from the dummy nest studies. There all three of the squirrels proved to have eaten pheasant eggs were young animals, and the eggs they ate were believed to have been intact. The smaller eggs of the bobwhite were consumed with equal facility by both age groups. Of the seven individuals offered bobwhite eggs, three did not eat them. Five eggs available for a total of 58 egg-days were unmolested.

GENERAL OBSERVATIONS

On June 14, a pheasant egg was placed near an occupied squirrel bur-

row; soon a young squirrel appeared and saw the egg. At first it acted frightened, then approached cautiously and sniffed at the strange object. This was repeated from three different directions. After four approaches, the animal went away satisfied, and never molested the egg in any way. Again, on August 22, pheasant eggs were being watched near some burrows. One squirrel which had appeared to be feeding on roots, finally found the eggs. It rolled, pawed, and played around with one for perhaps five or ten minutes, and had moved it about two feet, when taking alarm it ran into a burrow. The egg was not broken, nor was any attempt made to carry off or eat it. The other eggs all were in place.

A dozen local farmers were asked for their opinion regarding predation by ground squirrels on game bird nests. Seven had no ideas on the matter, three thought it was doubtful, and two suspected the squirrels would eat eggs; but none could recall any personal observations, or accounts of others.

Four farmers, however, claimed that these animals would steal chicken eggs. One related that one year his week-old chicks had been disappearing gradually. He caught one squirrel but the loss continued; finally he moved the hen house and found beneath it the remains of some chicks near the entrance to a burrow. He trapped another squirrel at the den and had no further losses of that kind.

Employees at the Corvallis State Game Farm said that a few years ago a digger squirrel was observed in a pen from which pheasant eggs had been disappearing. On one occasion, they killed a squirrel that was carrying a domestic hen's egg; it had been taking such eggs for some time. They said, also, that these squirrels will take young chickens. It is believed that some losses of young pheasants in the field rearing pens have been due to these animals, but no specific data are available.

CONCLUSIONS

1. In Oregon, the Douglas ground squirrel will eat eggs of the pheasant and bobwhite quail, and therefore is definitely a factor in nesting losses of these game birds in that region.

2. The intensity of these depredations is of considerable importance. The squirrels are active throughout the nesting season and find a large percentage of the nests.

3. They may eat the eggs at the nest but, more regularly, carry off single eggs and, in the latter case evidently make repeated return visits.

4. Observations and feeding experiments both show that only certain individual squirrels eat eggs; apparently they acquire a taste for the eggs. At times, a known "egg-eater" will ignore eggs.

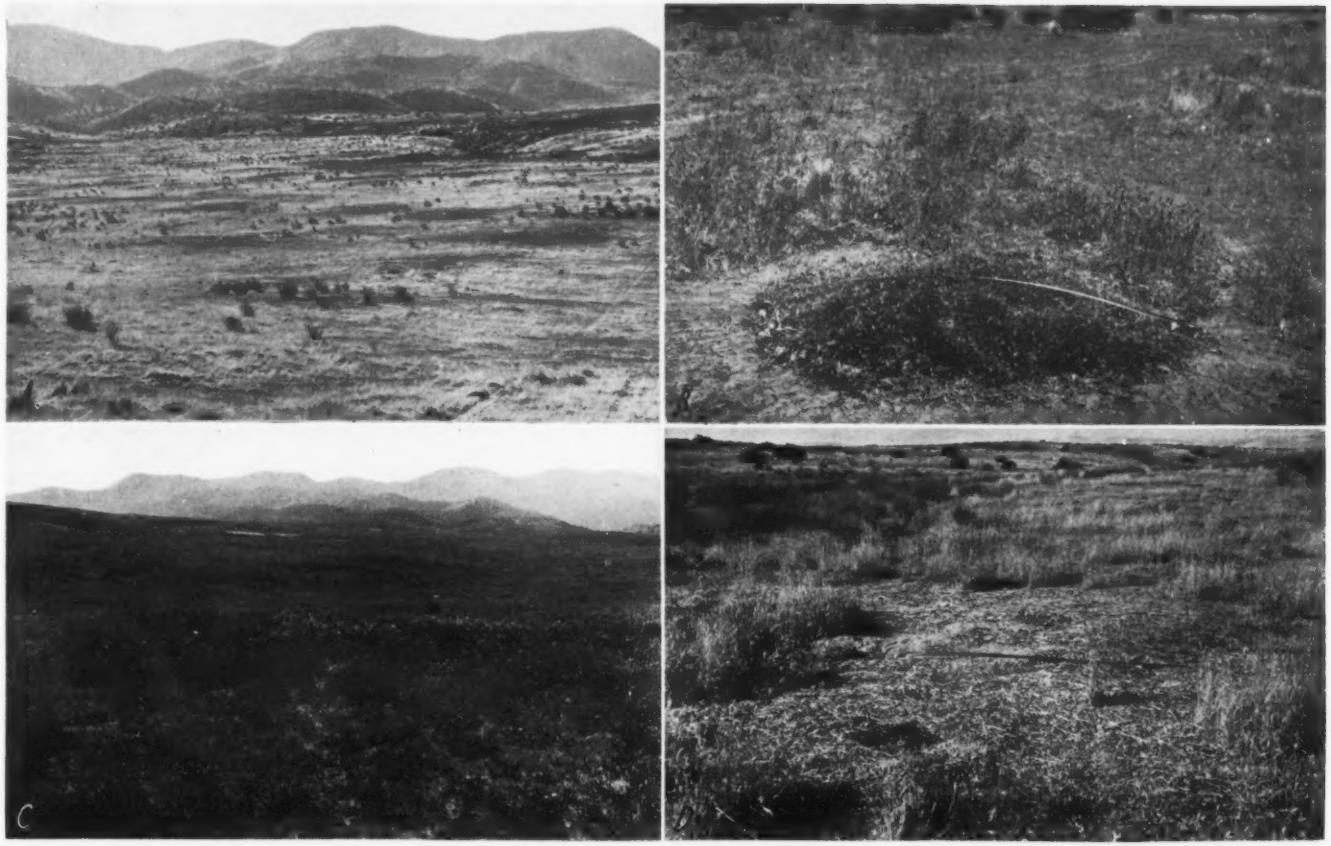
5. Nest raiding is not proved to be greatest in any one month.

6. Nests in proximity to squirrel burrows are particularly susceptible to destruction.

7. The degree of predation is not influenced by the naturalness of the habitat for game birds.

8. The size of the clutch apparently is not a factor in the probability of its discovery by a squirrel.

9. Nests in grass or cultivated crop cover are more likely to be destroyed than those in weeds or brush.



Work of the giant kangaroo rat (*Dipodomys ingens*). *A*. General view of habitat. Dark patches in center are the "precincts" cleared by kangaroo rats. In spring these are covered densely with vegetation (January 16, 1943). *B*. One haystack. (Surrounded by artificial dirt border to distinguish stack from adjacent dry grass); *Bromus rubens* immediately behind. *C*. Difference between undisturbed ground (foreground) and a rat precinct (immediately behind). A second stake (in the precinct) shows slightly behind and to the right of the first; both stakes 12 inches high (April 22, 1943). D. Area mowed by a giant kangaroo rat around its burrow (January 16, 1943).

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10. There is some indication that nests along fence rows are particularly vulnerable to predation.

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THE GIANT KANGAROO RAT AND SHEEP FORAGE

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During a study of the San Joaquin antelope squirrel, some interesting facts came to light in the life history of the giant kangaroo rat (*Dipodomys ingens*). Grinnell (1932) and Shaw (1934) studied the latter species in Fresno County, California, where Panoche Creek leaves the western foothills at an elevation of 500 to 600 feet and enters the San Joaquin Valley. The vegetation there is entirely annual, save in the creek bottom. My study was carried on six miles east of Panoche in San Benito County, California, and about six miles airline southwest of where Grinnell and Shaw worked. The elevation is 1,100 to 1,300 feet and most of the vegetation likewise is annual, but present also are joint pine (*Ephedra californica*), and occasional California juniper (*Juniperus californicus*), and snakeweed (*Gutierrezia californica*). Only the last of these extends over the whole study area (Pl. 8, A).

Grinnell emphasized the fact that he neither caught nor saw any other rodent within "*ingens*-owned" terrain. Shaw mentions a *Peromyscus*, but no other small mammal. In 167 trap nights I caught one *Dipodomys heermannii tularensis*, two *Onychomys torridus tularensis*, and two *Peromyscus maniculatus gambelii*, where joint pine was present; in the open country where only snakeweed was present nothing was caught. These three species were trapped near the *tularensis* side of the boundary between the habitats of *tularensis* and *ingens* (Tappe, 1941) but no small nocturnal mammal was seen in *ingens* territory. Of diurnal mammals, the San Joaquin jack rabbit (*Lepus californicus richardsoni*) was seen occasionally, and the San Joaquin antelope squirrel (*Citellus nelsoni*) was definitely resident in numbers. Certainly, as Tappe suggests for the Tulare kangaroo rat, other small mammals are scarce where kangaroo rats are abundant, but the antelope squirrel is an exception.

The squirrel is strictly diurnal and the rat nocturnal; perhaps the larger bulk of the squirrel reflects greater strength and aggressiveness. Four rats taken by Shaw averaged 148 grams, and 52 squirrels taken by me averaged 166 grams.

The antelope squirrels used burrows of the kangaroo rat, possibly abandoned or "duck-in" burrows. Occasionally a squirrel ran into an occupied hole, as evidenced by his rapid reappearance. Each squirrel seemed to have one certain hole to which it ran if possible; in most cases this was unmistakably of kangaroo rat origin. The extent to which the rats furnish the squirrels with burrows is unknown. The squirrels do some digging, but certainly depend largely upon the kangaroo rats for their shelters.

There seems to be little competition between these two rodents for food. During the late spring, summer, and early fall, the squirrels seem to depend largely upon insects, mainly a grasshopper (*Oedaleonotus enigma*); green and dry seeds of joint pine and seeds of red brome (*Bromus rubens*) and of red-stemmed filaree (*Erodium cicutarium*) make up the vegetative part of their diet. During the winter the dry seeds of the above three species plus any available animal matter seem to satisfy them. Early in the spring this is supplemented with newly growing red stemmed filaree, which soon becomes the main article of diet and continues so until the plants dry up in the heat of late spring. No stomach analyses were made on the kangaroo rat, but observations suggest that it subsists almost entirely upon seeds of red brome supplemented by those of filaree. It may consume more green material than can be determined indirectly because little cutting is seen. The mowing and shelling of red brome is apparently the main work and starts as soon as the brome begins to dry. The food preferences of the giant kangaroo rat thus appears to be much as Tappe found for the Tulare kangaroo rat, although my study was less thorough. Red brome, the main food of both rats and in part of the squirrel, is so abundant that many times the present rodent population could subsist upon it.

The three or four enemies present probably were common to all local rodents. Scats of the San Joaquin kit fox (*Vulpes macrotis mutica*) contained remains of the giant kangaroo rat, but none of antelope squirrel. The California badger (*Taxidea taxus neglecta*) was seen and many of its workings were in kangaroo rat precincts. Pellets of the barn owl (*Tyto alba pratincola*) examined by Tappe contained both species. One weasel (*Mustela* sp.) was frightened from a burrow system of kangaroo rat origin, but the rodent it was preying upon could not be determined.

Two rodents thus occupy the same habitat and may have the same enemies; the adults are both intolerant towards other species, but seemingly are able to live together, because they work on different "shifts."

This study of the kangaroo rat was made to learn the origin of "haystacks" (Pl. 8, *B*) in the squirrel study area. These stacks consisted almost entirely of separated heads of the red brome, and only two rodents might make such accumulations. On May 22, 1941, a frame of earth around a stack was smoothed; the next morning tracks and tail marks showed the presence of kangaroo rats. Over a long period of observation the squirrels were never seen to bother or show any interest in the stacks. I spent the night of May 19–20, 1942, near one stack; at 3:20 A.M. I turned on the automobile headlights and watched a kangaroo rat work

industriously near the stack and go into a nearby burrow. The animal appeared to be gathering and taking seed into its burrow. Neither species of rodent was seen to add or take material from a stack but I inferred the stacks were made by the rats because the activities of the rats were more directly connected with them. One rat that was shot had shelled seeds of red brome in its cheek pouches. From this I concluded that the curing season must be ended and the rat was then storing directly underground. On a third occasion (May 23, 1942) a kangaroo rat was watched while at work in a light beam. It began at 9:25 P.M. and work continued until daylight; every time I awakened it was at work.

These haystacks appeared to be curing places or temporary surface caches, one to each rat. The grass was nearly or entirely dry when plucked and piled in stacks about 4×2×24 inches overall. One large stack measured 4 by 6 feet and was 4 inches deep. None was found in the Valley by Shaw or Grinnell, but their observations were not made in the late spring and summer when the stacks are made. (Dr. Shaw tells me that since his paper was written he has noticed stacks in the area where he worked.) In Shaw's list of foods of the giant kangaroo rat, peppergrass (*Lepidium nitidum*) was the main item and red brome was found only once. I found no peppergrass at the 1,200-foot level and Tappe indicates that it was unimportant in the diet of the Tulare kangaroo rat. The fate of these stacks is unknown; some disappear as if removed. Others, perhaps belonging to rats that are killed or die, remain to be dispersed later by wind, rain, and sheep. Two underground caches contained a mixture of sand and red brome, and another was comprised mostly of filaree seed.

The giant kangaroo rat has an interesting effect on the vegetation in the area studied. The dens and burrows generally are on high spots of hillsides, or else the tops of "hog-wallows" in flat country; occasional diggings occur in low spots. During the growing season of late winter and spring, the precinct of each animal was well covered with filaree and red brome to a height of six inches or more (Pl. 8, *C*), but intervening spaces had only a sparse cover (1½ inches tall) of the same plants. The occupied and unoccupied areas differed greatly; the former was broken and disturbed—cultivated in a sense—whereas the intervening spaces were hard, packed by rain and countless sheep.

Filaree, the best sheep food in the area, seems to grow better where the earth has been disturbed; and water, so vital in this country, seems to penetrate better, with less run-off, in these spots than in harder ground. The seeds of filaree seed may be able only to enter soft ground easily. This vegetational difference in respect to filaree lasts for some time; areas about burrows long unused still support good growths although eventually they probably wear away. Hillocks showing no signs of ever having been occupied are practically devoid of cover. Intervening areas disturbed by other agencies also may have good cover, hence differences in the soil apparently are not responsible for the better growth. Occasional hillsides are well covered with red brome, which lasts longer in the spring and puts on more growth after the filaree is gone. Much of the area is covered with a fair

growth of brome, but not as dense as on the hillocks. Upon looking over the region from an elevation, these dark green spots stand out in contrast to the sparser areas of light green. Grinnell (1923) accorded the burrowing rodents a role in soil formation, and in this case we may (reasonably) give them a place in plant propagation.

The local sheep feed extensively on the kangaroo rat precincts and continue long enough on each hillock to about mow it clean, but they waste little time on the poorer intervening spaces. An average plot two feet square in the unbroken spaces yielded 70.5 grams of green material, whereas one of the same size in a rat precinct yielded 400.1 grams. On some areas 50 per cent of the land was covered with better growth resulting from rodent work. These spots also remain green longer than the intervening spaces which, to begin with, are hard and nonabsorbent. Locally there was poor forage production in 1943; save for a little red brome the only real feed for sheep was on the rat precincts.

The kangaroo rats also have an effect on the red brome grass (Pl. 8, *D*), which plant is the main constituent of their haystacks and probably their main food. Evidently a rat methodically clears off the brome around its burrow and gradually broadens the circle until a large area is cleared. On one acre, which faced equally south and north, the south-facing portion had seven precincts, each a cleared area of about 15 by 20 feet, and the north-facing slope had three of about the same size. There was also some miscellaneous cutting on the top of the ridge. On other slopes and flats examined December 16, 1942, 50 per cent of the vegetation was gone from some but on others was untouched.

The effect on the general vegetation and of this in turn on grazing is not clear. Certainly the lusher growths of filaree and succulent red brome, from late February to early May, resulting from the work of the kangaroo rats, are valuable as ground cover and unexcelled as feed for sheep. The red brome is cut by the rats from May until the next growing season; it is less valuable for sheep than filaree but serves, along with concentrates, to carry them in the autumn, when they return from high mountain pastures or grain stubble fields, until green feed starts. It also serves as ground cover to protect the soil. The kangaroo rat, of course, utilizes some of the green vegetation, but apparently not enough to make any appreciable difference during the growing season. On the whole, the effect of the giant kangaroo rat appears to be beneficial to the local sheep industry. The small amounts of perennial grasses (*Stipa pulchra*, *Sitanion hystrix*, and *Poa scabrella*) present do not seem to be utilized by either sheep or kangaroo rats, although the few plants found are lush and healthy.

This study was made in a limited are and much of the range of this kangaroo rat elsewhere does not appear to be affected in the same way. The two species of plants most affected are introduced annuals; the study does not indicate what effect this kangaroo rat may have had on the perennial grasses originally native.

R. M. Bond and W. T. Shaw read and commented on this report, and C. H. Quibell checked the plant identifications.

SUMMARY

The giant kangaroo rat and San Joaquin antelope squirrel occupy the same territory but do not compete; the former is abroad at night and the latter during the daytime.

The cultivating action of the kangaroo rat increases the amount of red-stemmed filaree and red brome grass more than five times thus creating more sheep feed where greatly needed. The portions of land thus cultivated remain green longer in the season.

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COLOR, SEX RATIOS, AND WEIGHTS OF MARYLAND MUSKRATS, II[1]

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Investigations on Maryland muskrats (*Ondatra zibethica macrodon*) at the U. S. Fur Animal Field Station, Blackwater National Wildlife Refuge, Cambridge, Maryland, began in 1937. The present phases of the study commenced in 1941 when definite trapping units were established for the Refuge, totaling 5,233 acres of suitable marsh and comprising 27 "hunts."

The boundaries of these units are maintained so that data on the abundance and type of food, color and sex ratios of muskrats, over-population and disease and their effects on weight averages and pelt quality, predation, and the effects of controlled burning operations can be compared over a period of years. These factors have vital application to practical and intelligent trapping and marsh management.

[1] Leonard M. Llewellyn assisted in the computation and analysis of the data involved.

Details on the color, sex ratios, and weights of 9,895 muskrats obtained in 1941 (January 1 to March 15), and a review of literature on the subject, were published by Dozier and Allen (Journ. Wildl. Mgt., 6, 294–300, 1942). The present paper is a report on the 1942 trapping season, when 6,735 muskrats were taken from the same areas (Table 1). This total is 32 per cent below that of the preceding year and represents a continuing downward trend from the peak population in 1938.

Difficulty was again experienced in separating some of the larger kits and small adults, hence all individuals weighing 1 lb. 6 ozs. or less were arbitrarily classified as kits to retain uniformity of treatment. It becomes increasingly evident, however, that weight alone is not a good criterion for age classification.

Of the catch in 1942, 6,496 were considered to be adults and only 239 as

TABLE 1.—COLOR AND SEX OF ADULT MUSKRATS TRAPPED ON THE BLACKWATER NATIONAL WILDLIFE REFUGE, 1942

Unit No.	Total catch	Brown		Black		Percentages		Ratio of males per 100 females
		Males	Females	Males	Females	Brown	Males	
1	226	81	51	60	34	*58*	*62*	168
2	298	85	55	96	62	*47*	*61*	141
3	321	88	79	66	88	*52*	*48*	88
4	322	81	56	105	80	*43*	*58*	137
5	145	41	24	44	36	*45*	*58*	138
6	244	60	49	74	61	*44*	*55*	122
7	303	63	59	102	79	*40*	*54*	119
8	265	49	45	85	86	*35*	*51*	102
9	171	63	26	50	32	*52*	*66*	195
10	523	155	110	150	108	*51*	*58*	140
11	62	11	13	18	20	*39*	*47*	88
12	373	118	78	93	84	*53*	*57*	130
13	181	44	43	56	38	*48*	*55*	123
14	178	42	34	62	40	*43*	*58*	140
15	369	138	75	91	65	*58*	*62*	164
16	660	237	137	164	122	*57*	*61*	154
17	285	95	54	95	41	*53*	*67*	200
18	28	7	5	8	8	*43*	*54*	115
19	119	38	14	43	24	*44*	*68*	213
20	137	40	17	59	21	*43*	*72*	260
21	218	63	42	72	41	*48*	*62*	163
22	139	37	27	46	29	*46*	*60*	148
23	188	36	53	54	45	*47*	*48*	92
24	184	46	28	71	39	*40*	*64*	175
25	89	17	22	37	13	*44*	*61*	154
26	90	20	20	37	13	*44*	*63*	142
27	225	76	55	60	34	*58*	*60*	153
Totals	6,343	1,831	1,271	1,898	1,343	*49*	*59*	143

kits. The black color phase again predominated slightly over the brown. The combined catch of adults and kits comprised 3,272 brown and 3,463 black animals (49 to 52%) as against that in 1941 of 4,591 brown and 5,304 black (46 to 54%). Local variation again was strongly evident, and the percentage ratios for both color and sex fluctuated considerably from those of the previous season on most of the trapping units. In 1942, the lowest color ratio was 35 per cent brown to 65 per cent black (Unit 8) and the highest was 58 to 42 (Units 1, 15, 27).

For 6,343 adults on which both color and sex data were obtained (Table 1), Fisher's "Z" test showed that differences between the numbers of brown and black animals were not significant, whereas differences between the various units were highly significant (more than 99:1).

SEX RATIO

The 1942 data clearly showed preponderance of adult males over females and a slight increase in the percentage of the former. These differences were highly significant as were the variations between the units.

The sex was determined accurately for 238 of the 239 kits taken in 1942; these were 114 (48%) males and 124 (52%) females, agreeing rather closely with the ratio of 205 (46%) males and

245 (54%) females in 1941. The fact that in both years the female kits outnumbered the males, while in the adults the opposite was true, lends support to the possibility that the sex ratio of adults may not be the same as that at birth.

Table 2 records the sex ratios of the catch by months and shows conclusively that the preponderance of males over females was maintained throughout the trapping operations in both years. It also shows that 60 per cent of the total catch in 1941 was obtained during the first month in contrast to 45 per cent during the same period in 1942.

TABLE 2.—SEX RATIO OF PART OF THE MUSKRAT CATCH (ADULTS AND KITS) ON THE BLACKWATER NATIONAL WILDLIFE REFUGE, 1941 AND 1942.

	1941 Catch		*Percentage of males*
	Males	*Females*	
January	3,327	2,534	*57*
February	1,110	1,029	*52*
March 1–15	978	776	*56*
Totals	5,415	4,339	*56*

	1942 Catch		*Percentage of males*
	Males	*Females*	
January	1,746	1,234	*59*
February	1,175	899	*57*
March 1–15	942	626	*60*
Totals	3,863	2,759	*58*

WEIGHTS

Weights were obtained on 6,343 adults during 1942; those of any partly eaten by predatory or scavenger birds and mammals while in the traps were discarded. The 1,831 brown males aver-

TABLE 3.—AVERAGE WEIGHTS (POUNDS) OF MUSKRATS CAUGHT ON THE BLACKWATER NATIONAL WILDLIFE REFUGE BY TRAPPING UNITS, 1942

Unit No.	Brown		Black		All individuals
	Males	Females	Males	Females	
1	2.5	2.2	2.5	2.2	2.4
2	2.6	2.4	2.5	2.3	2.5
3	2.5	2.4	2.8	2.4	2.5
4	2.5	2.3	2.4	2.1	2.4
5	2.5	2.4	2.3	2.2	2.3
6	2.4	2.2	2.4	2.3	2.3
7	2.6	2.2	2.4	2.3	2.4
8	2.2	2.1	2.2	2.1	2.4
9	2.3	2.1	2.2	2.1	2.2
10	2.2	2.2	2.3	2.1	2.2
11	2.3	1.9	2.4	2.1	2.2
12	2.3	2.1	2.2	2.1	2.2
13	2.0	2.0	2.1	2.1	2.1
14	2.2	2.1	2.2	2.1	2.2
15	2.1	2.0	2.1	1.9	2.1
16	2.3	2.1	2.2	2.2	2.2
17	2.1	1.9	2.0	1.8	2.0
18	2.0	2.0	2.2	1.9	2.0
19	1.9	2.0	2.1	2.0	2.0
20	2.2	2.1	2.3	2.1	2.2
21	2.4	2.3	2.4	2.2	2.3
22	2.4	2.2	2.4	2.3	2.3
23	2.4	2.3	2.4	2.2	2.3
24	1.9	2.2	2.4	2.1	2.3
25	2.3	1.9	2.3	2.1	2.2
26	2.2	2.2	2.3	2.0	2.2
27	2.4	2.3	2.4	2.3	2.4
	2.3	2.2	2.3	2.2	2.2

aged 2.3 pounds (1,043) grams) and 1,271 brown females, 2.2 pounds (998 grams); the 1,898 black males also averaged 2.3 pounds and 1,343 black females, 2.2 pounds. These averages are identical with those reported for 1941 on 9,311 adults. The average weight of all adult males was 2.3 pounds (1,043 grams) and of the females 2.2 pounds (998 grams), showing that the males are consistently heavier than the females.

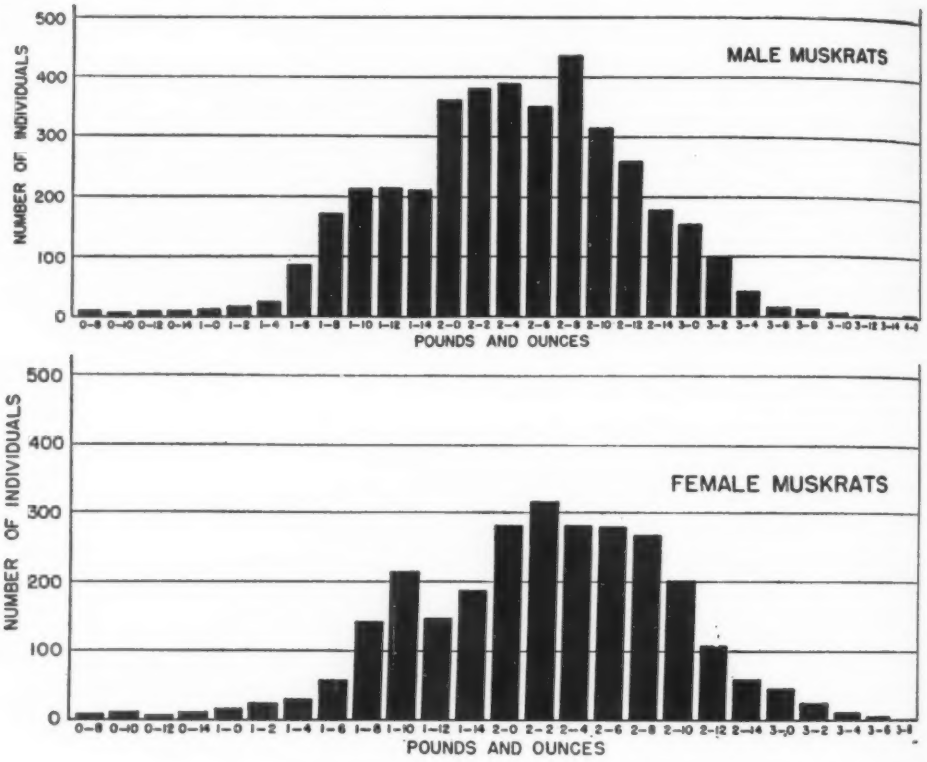

Fig. 1. Numbers of male and female muskrats by weight groups, Blackwater National Wildlife Refuge, 1942.

These weights are summarized by units in Table 3. Differences in weight between black and brown animals and the sexes are not significant. As in 1941, muskrats from the trapping units varied considerably in average weight and these differences between the various units are highly significant. The low averages were recorded from units poorest in amount and quality of food plants and the highest from those best supplied. The character and abundance of food plants on each of the units again were noted during the annual house count, made during November and December, preceding the trapping season.

The largest muskrat taken during the 1942 season, and in fact since the establishment of the Station on this Refuge in the autumn of 1937, was an old brown male weighing exactly 4 pounds. This individual probably ap-

proached close to the maximum weight and age for the local race, *Ondatra z. macrodon*. It was trapped on the Colston Pond marsh (Unit 3) in a solid stand of three-square (*Scirpus olneyi*) on February 18. When skinned, the fresh pelt weighed 12 ounces.

Figure 1 shows the distribution of the muskrats trapped in 1942 by 2-ounce weight groups as was done in the previous paper. The 2-pound 8-ounce group contained the largest number of males and the 2-pound 2-ounce group the largest number of females, all thought to be adults more than a year old. These data differ considerably from those for the 1941 catch in which the largest numbers of both sexes were in the 2-pound 6-ounce group. Such differences are undoubtedly due in part to seasonal variation affecting the various periods or waves of breeding.

SURVIVAL ABILITY OF COLOR PHASES

There is a belief among trappers and those who have handled large numbers of the Maryland muskrat that the brown rat is hardier and can stand more abuse than the black phase. Data obtained during 1941 on kits showed 209 (46%) brown to 241 (54%) black and for adults 4,357 (47%) brown to 4,954 (53%) black. Similar figures for 1942 on kits showed 109 (46%) brown to 130 (54%) black, and for adults 3,163 (49%) brown and 3,333 (51%) black. These figures would seem to indicate only a slightly higher survival rate, if any, for the brown animals.

SUMMARY AND CONCLUSIONS

The 1942 catch of 6,735 muskrats on the Blackwater National Wildlife Refuge represented a decline of 32 per cent from the catch in 1941. There were 6,496 adults but only 239 kits (1 lb. 6 ozs. or less), a distinctly smaller percentage of kits (3.5%) than that reported for the 1941 catch (4.5%).

The black color phase again predominated slightly over the brown but the difference was not significant. There were 3,373 brown and 3,463 black animals (49 to 51%) as against the 1941 catch of 4,591 brown and 5,304 black (46 to 54%). Differences in color between the various trapping units appeared highly significant.

The sex of 6,384 adults and 239 kits in 1942 was determined accurately. The adults comprised 3,749 (58%) males and 2,635 (42%) females; the kits 114 (48%) males and 124 (52%) females. There was an adult ratio of 143 males per 100 females and the larger number of males was highly significant. Tabulation of the male to female ratio by months shows conclusively that the preponderance of adult males over adult females was maintained throughout the trapping operations in both years.

Weights were obtained for 6,343 adults. The average for all adults was 2.2 pounds (998 grams); 1,831 brown males averaged 2.3 pounds (1,043 grams), and 1,271 brown females 2.2 pounds (998 grams); 1,898 black males averaged 2.3 pounds and 1,343 black females 2.2 pounds. These averages are identical with those reported for 1941 on 9,311 adults. The average weight for all adult males was 2.3 pounds and for females 2.2 pounds, showing that males are consistently slightly heavier than females. Differences in weight between the brown and black color phases and between the sexes are not significant.

BRIEFER ARTICLES

LOTUS CONTROL

The American lotus (*Nelumbo lutea*) is so abundant in eastern Texas that it occasionally becomes a pest and fishing with an artificial lure becomes impossible in dense growths. Its value as duck food is negligible in comparison with other plants. Control of this lotus is simple, however, by spraying a fine film of oil on the leaves, when the plants will die. It is best to use equipment with a fine spray-nozzle attachment and to work on a hot, clear day. Any kind of lubricating oil is effective, but a mixture of two parts of used oil to one part of kerosene is most economical.

In a large-scale eradication program approximately three 55-gallon drums of this mixture were used per acre for dense stands of lotus. The oil generally can be obtained free at any gasoline filling station and kerosene can be purchased for ten cents a gallon. The total cost of materials for treating one acre therefore was $5.50.

By directing a fine film of oil at the leaves only, there is no danger of polluting the water. The leaves of the lotus died within one day after application of the oil and within a week the plants were rotten down to the roots.—Hilbert R. Siegler, *Texas Game, Fish and Oyster Commission, Austin, Texas.*

DETERMINING THE AGE OF PINNATED AND SHARP-TAILED GROUSES[1]

Wright and Hiatt (Auk, 60: 265–266, 1943) separate immature grouse (in their first autumn) from adults (one year or more old), on characteristics of the primaries. Grouse retain the two outer primaries in the post-juvenal molt but adults lose all primaries during the post-nuptial molt.

I used this criterion on grouse shot during the hunting season (October) in Michigan, when many of the birds are still molting. Since this criterion is good only while molt is in progress, its usefulness is limited. While investigating the status of pinnated grouse (*Tympanuchus cupido*) and sharp-tailed grouse (*Pediocetes phasianellus*) in Michigan I sought reliable plumage characters to differentiate immatures from adults after the molt.

Various methods have been tried by "chicken" workers but no plumage character yet published is reliable as an indicator of age (Prairie Grouse Cooperative Study, Progress Report No. 5, p. 34). The criteria include the shape of the outer primaries and primary coverts and the relative abundance of light bars or spots on these feathers. I have used these plumage characters with varying success and have concluded that they are not consistent. A difference was noticed, however, in some primaries of the adults as compared to those of immatures (age determined by bursa of Fabricius); this seems more satisfactory than any other plumage character I have used on prairie grouse and may, therefore, be of interest to other "chicken" workers. For convenience in this discussion, the outermost or distal primary is called the first and the others are numbered successively toward the inner portion of the wing.

Briefly, the method is as follows: With thumb and forefinger arrange the barbs at the tips of the second and third primaries, if they are ruffled, by stroking them gently toward their distal ends. Then view them in silhouette against a light or the sky and compare the tips of the second and third primaries. A low-power hand lens is helpful in a few cases, but usually is not necessary.

[1] Contribution from Pittman-Robertson Wildlife Restoration Project 5-R, Michigan Department of Conservation. Helpful advice and criticism was given by F. N. Hamerstrom, University of Michigan, and members of the Game Division, Michigan Department of Conservation.

Three outer primaries of sharp-tailed grouse. *Above.* Immature, showing contrast between frayed tip of second primary and even, unbroken tip of third primary (bird determined as immature by presence of bursa of Fabricius). *Below.* Adult, showing even, unbroken margins at the tips of *both* second and third primaries (determined as adult by absence of bursa of Fabricius).

On immature birds the comparatively worn appearance of the tip of the second primary, as evidenced by broken barbs resulting in an uneven feather margin, is usually in sharp contrast to the smooth, unbroken margin of the tip of the third primary (Pl. 9). Adult birds, on the other hand, exhibit little or no wear on the tips of either the second or third primary; if they do show wear, it will be approximately equal on both feathers. In addition, the first two primaries of the immature bird often appear paler than the other primaries, when examined in good light, while in the adult there is no discernible difference in shade between any of the wing feathers.

The differential wear of the second and third primaries of immature "chickens" sometimes is quite evident even before the post-juvenal molt is complete, affording a good check with the method described by Wright and Hiatt.

There are two probable factors responsible for the apparent differential abrasion of these feathers: the second primary of the immature bird is present at least one month longer than is the third primary, and the second primary of the immature possibly becomes worn at a faster rate than the third. The latter statement is substantiated by the fact that many birds exhibit a tendency for juvenal and immature feathers to become worn and faded more rapidly than the corresponding feathers of adult plumages.

It should be emphasized that what is true of the second primary is also true of the first, and what is true of the third primary is also true of the fourth and subsequent primaries. The second and third are chosen for comparison in preference to any others because they are nearly alike in size and shape, and are conveniently adjacent. Also, the first primary, probably because it is shorter than the second, usually does not become as badly worn at the tip as the latter.

It is easiest to determine age by this method in winter; in autumn some birds do not exhibit sufficient wear on the tips of the primaries, while in spring and summer many birds, particularly cocks, show too much wear. Captive specimens, even if confined for only a short while, muss up their primaries so much that this method cannot be used. It was used successfully, I believe, by myself and some of my associates in judging ages of more than 200 prairie grouse live-trapped during the winter.

The validity of the above outlined method for age determination may be questioned on the ground that insufficient proof is presented. From personal experience with at least 50 live birds, over 100 dead specimens in the flesh, and three or four hundred museum "skins," I feel confident that it is valid. It should, of course, be checked against the bursa and the primary molt criteria whenever possible.

I have noted a similar differential wear of the primaries in museum specimens of the wild turkey and sagehen, and the sooty, blue, and spruce grouses. The method was unsatisfactory with ruffed grouse. In some instances I judged immatures or adults of ruffed grouse correctly (checked by the bursa method), but in a majority of cases age determination would have been merely a guess. Failure of the method with this species may be because the feathers are soft and flexible, hence subject to comparatively little wear.—GEORGE A. AMMANN, *Department of Conservation, Lansing, Michigan.*

NEWS NOTES

The Ninth North American Wildlife Conference will be held in Chicago at the LaSalle Hotel, April 24 to 26, 1944. All sessions will emphasize better coordination of conservation activities, present and post-war. The technical sessions and chairmen are: April 24—*Fish management*, H. S. Swingle, Alabama Agricultural Experiment Station, Auburn, Ala.; *Big game management*, D. I. Rasmussen, Utah Cooperative Wildlife Research Unit, Logan, Utah; April 26—*Upland game management*, F. C. Edminster, Soil Conservation Service, Upper Darby, Pa.; *Waterfowl management*, F. C. Lincoln, U. S. Fish and Wildlife Service, South Interior Building, Washington 25, D. C. Those wishing to present papers should correspond directly with the chairman concerned promptly (limiting date, March 20) sending title, one-page summary, and conclusions. Authors of accepted papers will receive further instructions from their chairmen. Papers should not average more than 1500 words. No projection facilities will be provided, but contributors may supply their own if desired. Lloyd W. Swift, U. S. Forest Service, South Agriculture Building, Washington, D. C., is general chairman for the technical sessions.

The annual meeting of the Wildlife Society will be held during the conference.

Withdrawal of many members and associates of our Society into the armed forces and war industries is reflected in the decreased number of manuscripts submitted for publication. The recent supply of accepted papers is such that prompt publication, within about six months, usually is possible. There seems to be a dearth of papers on fish and fisheries in recent months; suitable articles in this field are needed. Limitations by the War Production Board as to the quota of paper available have as yet had no serious effect on this Journal in respect to publication of manuscripts.

A list of members and associates of The Wildlife Society now in the various services and their latest mail addresses is planned for the next issue. Members are asked to write *at once* to the Editor, giving this information for any of their colleagues or friends to supplement such records as the Secretary is able to provide.

When *Wildlife News* was suspended, it was expected that members would supply news notes, for the Journal; only one such communication has been received, comprising three items.

Weston J. Donehower (Lt., Naval Intelligence) has been in action in the South Pacific, has been down at sea on a rubber raft, and has received both a personal and a group citation for his work in action.

William E. Zimmerman (Capt., Air Force Intelligence) of the 12th Air Force Support Command has been in the North African, Sicilian, and Italian campaigns. His letters to F. C. Edminster include various comments pertaining to conservation matters in those areas.

J. Victor Skift (New York State Conservation Department), former Superintendent of Inland Fisheries, has been made Deputy Commissioner of the Department.